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STUDIES IN PALEOZOIC CORALS

BRANDON H. GROVE

I. Introduction

During the past century our knowledge of corals has been built up from the contributions of many men in many lands. The complete picture thus constructed, however, can only be perceived when its various units have been translated into a common tongue and presented as a coherent whole. A critical review of this sort was made by Jules Haime in 1860, in the first volume of Milne-Edwards' *Histoire Naturelle des Coralliaires;* and the studies of the following decade were similarly summarized by De Koninck in his *Animaux Fossiles du Terrain Carbonifere de la Belgique.* (1872). The years subsequent to De Koninck's writings have probably been those most significant in the study of corals, but few authors have paused to summarize the numerous data resulting from these researches, and, further, the best of these exacting surveys have been made in languages other than English.

It is hoped, therefore, that the historical summary offered in Part I of the present paper will prove of value (1) in presenting the general data available to modern students, (2) by indicating the sources of detailed studies for those interested particularly in restricted fields, and (3) by offering a brief survey, in English, of the many works available only in foreign tongues.

I am indebted to Professor Carey Croneis, of the University of Chicago, for suggesting the present study, and for his continued counsel and guidance in the present work. My sincere thanks are also due to Mr. A. W. Slocum, of Walker Museum, University of Chicago, whose suggestions in the matter of technique have been invaluable, and to the curators of Walker Museum, who have made available the splendid examples of Mississippian corals afforded by the Miller, Sampson, Weller, and Gurley collections.

II. A Summary of Modern Studies in the Paleontology of Corals

INTRODUCTION OF MODERN TECHNIQUE

Laurent De Koninck, penning the introduction to his *Nouvelles Recherches sur les Animaux Fossiles,* published in 1872, expressed deep regret that he

was unable to avail himself of the results of the newly inaugurated study of corals by means of their thin sections. This study was then in the hands of committee appointed in 1868 by the British Association for the Advancement of Science. Monsieur De Koninck politely expressed the hope that the skill and ardor of the committee, composed of James Thomson, Henry Woodward, and R. Harkness, would more than suffice to overcome the great technical difficulties of their task. His apprehensions regarding the complication of the work, however, seem to have been well founded, for in his first report to the British Association, in 1869, James Thomson had announced that although several hundred corals had been sectioned, most of them had been so crushed and fractured that they were useless for their purpose. Indeed, in one lot of eighty-seven corals, only two sections were sufficiently perfect to warrant being photographed. The time and labor involved in the cutting, examining, and finishing of sufficiently perfect sections made it impossible to produce a complete set within a year. In addition, the photographs themselves, made by the then current process, soon faded upon exposure to light. Therefore the hope was expressed that a new carbon process would be an improvement, and also that they might soon be able to produce fac-similes on zinc or copper plates.

During the second year of the committee's existence it made much greater progress, and at the meeting of the British Association in 1870 it exhibited nine photographic plates presenting sections of the genera *Amplexus, Zaphrentis, Cyathophyllum, Campophyllum, Clisiophyllum* and *Cyclophyllum*. Referring to this latter genus, the committee emphasized the importance of employing thin sections in the study of corals by the following statement:

> "The history of this specimen is perhaps one of the best illustrations on record showing the necessity of carefully working out the details of fossil corals before they receive either generic or specific names. It was named *fungites* by Ure in 1793, *Turbinolia fungites* by Fleming in 1828, *Cyathophyllum fungites* by Geinitz in 1845, *Clisiophyllum prolapsum* by McCoy in 1849, *Aulophyllum fungites* by the same authors in 1851 who named it *Aulophyllum prolapsum* in 1845, viz. Milne-Edwards and Haime. This great diversity of nomenclature we can only attribute to the fact that non-essential and external characteristics have been too implicitly trusted in drawing generic distinctions; when we examine their internal structures, genera named exhibit essential differences of conformation" (1870, pp. 43-44).[1]

In its third report, in 1871, the committee again emphasized the difficulty it was meeting in the too frequent crushing and fracturing of its specimens during the processes of cutting and grinding. It announced, however, that much better results had been achieved in photography, and that it had been successful in transferring even the finest details of the sections to copper plates, making them available for extensive publication in the future.

By 1872 this careful study and comparison of the internal characters of hundreds of specimens was beginning to bear fruit in other than purely technical ways. The report of the committee for this year contains a lengthy morphological study, with recommendations as to which of the structural fea-

1 References are given by means of the chronologic position of the work cited in the alphabetic list of authors to be found in the bibliography at the close of the paper.

tures of corals were of probable generic and specific significance. The presence or absence of a columellarian line, and of endothecal dissepiments, were considered inadequte for specific determinations. Among the 156 established species of British fossil corals, they found the existence of between 300 and 400 varieties, the increase in the number of varieties over those previously known being so great, and the variations so minute, that they found difficulty in determining just what constituted specific characters. Their conclusions regarding this difficulty, and their suggestion for a solution, are of some interest:

"The gradations of the varieties are in some cases so constant, and pass so imperceptibly into each other, that they induce the inference that there has been an inherent tendency in the polyp to vary independent of, but to be modified by, the conditions of its surroundings. . . . In order that some definite rule may be obtained as a guide in the classification of corals, it is proposed to select generic types, and, after making sections of these through different parts, to exhibit their structure in plates, from the ova to the mature form; and it is only when this is faithfully done that we can hope to determine where a species begins and a variety ends." (1872, pp. 242-243).

The British Association was sufficiently impressed with the importance and potentiality of the work to continue its grant to the committee, and to augment its numbers by the appointment of Thomas Davidson and P. Martin Duncan, the latter of whom had just completed his important monograph on the Tertiary corals of Great Britain.

In its fifth and final report, in 1873, the committee exhibited an extensive series of plates showing serial sections of a wide variety of genera, but dealing particularly with species and varieties of *Zaphrentis* and *Amplexus*. James Thomson was assigned the task of publishing and elucidating the data and plates resulting from these five years of research by the committee.

Although hardly of more than secondary importance in itself, this work of the British Association's committee merits thoughtful recognition, not merely as a pioneering effort in the use of thin sections, but because it marks the introduction of modern scientific method into the paleontology of corals. So long as workers confined their attention only to form and features visible externally they dealt with ephemeral characteristics, susceptible only to general description. With the introduction of the exact data afforded by serial sections, however, there came the possibility of truly scientific discussion of ontogeny and phylogeny, morphology, and taxonomy, and the accurate comparison and delineation of genera, species, and varieties. The paleontology of corals came a step closer to being an exact science.

Morphological Studies

While the British scientists were thus engaged in shaping a new tool for the study of corals, the morphological discoveries of the French and German workers were preparing the way for its efficient employment. The labors of A. Kunth, in Germany, were of outstanding significance in this respect. To Kunth we owe the recognition of the mode of septal insertion peculiar to the tetracorals, formulated in the law which bears his name. (1869). Prior to

Kunth's studies it was not recognized that tetracorals differed from hexacorals in the manner in which new septa were added with continued growth. In fact the general rules for septal insertion worked out by Milne-Edwards and Haime, (1860, vol. I, pp. 48-51), were assumed to be equally valid for both the Tetracoralla and the Hexacoralla. As can be seen from the diagram of figure 1, the septal scheme of Milne-Edwards and Haime is based upon the assumption of radial symmetry in all corals, and the postulation of six primary septa. New septa are then inserted in groups of six, or multiples of six.

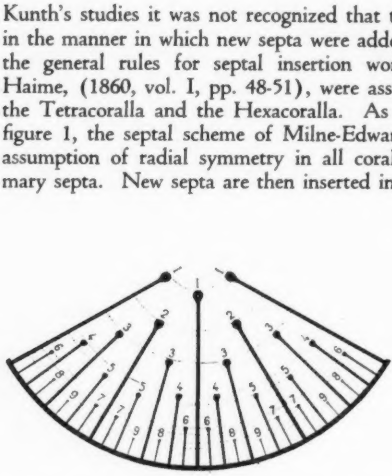


Fig. 1. Scheme devised by Milne-Edwards and Haime for septal insertion in corals.

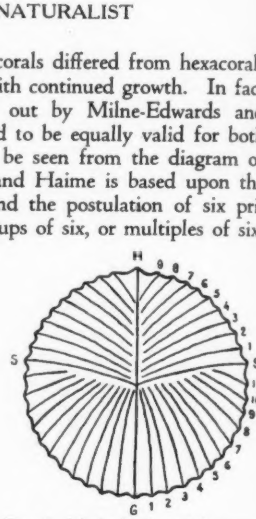


Fig. 2. Method of septal insertion in the Tetracorals accordinto Kunth.

The researches of Kunth showed for the first time that the arrangement of the septa among the tetracorals is not in acordance with a radial, but with a bilateral symmetry. He thus made available a criterion of the highest morphological value, for this disposition of the septa is characteristic of all the tetracorals, and stamps them unmistakably.

Kunth reached his conclusion largely by making a careful study of the stripes or ribs reflected onto the external portion of the corallum by the septa, but a similar conclusion can be drawn from a study of the arrangement of the septa within the cup itself. In a diagram of figure 2, the lines *h*, *s*, *g*, and *s* represent the four primary septa of a tetracoral. In the absence of other data, they may be recognized by the fact that the lines which they reflect upon the exterior of the cup extend all the way to the tip, showing that these septa were formed in the very earliest stages of growth. Of these four primary septa, *h* is designated the *cardinal septum*, *g* the *counter septum*, and both the septa designated as *s* are *alar septa;* the two quadrants of the cup which lie between the cardinal septum and an alar septum are called cardinal quadrants, and those enclosed by an alar septum and the counter septum are called counter quadrants.

In the light of these definitions, Kunth's law of septal increase may now be expressed as follows: In the cardinal quadrant all the secondary septa originate ajacent to the cardinal septum, and in time take up a position parallel to the alar septa; on the other hand, in the counter quadrants all the secondary septa originate adjacent to the alar septa, and take up a position parallel to the

counter septum. As a result, in the cardinal quadrants the secondary septa lying next to the cardinal septa are the youngest, and those lying closest to the alar septa are the oldest. In the counter quadrants the oldest secondary septa lie next to the counter septum, and the youngest are closest to the alar septa. There is thus a bilaterally symmetrical septal arrangement.

The fundamental importance of Kunth's discovery was greatly enhanced by the introduction of the technique of serial sectioning, which permitted a detailed study of the initial stages in the growth of a coral, and thus allowed the fullest application of morphological knowledge. An even deeper insight into the initial stages of coral development was given by the accurate studies of Lacaze-Duthiers upon living corals. In consequence of his research upon Actinarians, this author was able to publish, in 1872 and 1873, a survey of the earliest events in the secretion of a corallum and the development of the septa. (1872, 1873).

Lacaze-Duthiers introduced his studies by reviewing the works of the more important writers who had preceded him, notably Milne-Edwards and Haime, Schneider and Rötteken, and C. Semper. He concluded that in the writings of each of these authors there existed a common weakness. With each of them the interpretation of the sequence of events occurring in the development of a coral was based upon the relationship of its parts at the time of observation. From studies of this sort Milne-Edwards and Haime, and Schneider and Rötteken, had gained the belief that septa originate in cycles, of successively younger orders, and had worked out elaborate rules to account for this cyclic insertion of septa. Semper, who studied living forms, cast some doubt upon this conception by showing that it was subject to numerous exceptions, but he did not attempt to refute it. After a prolonged study of the development of both soft and stony corals, from the embryo to the adult form, Lacaze-Duthiers found that in neither the formation of the mesenterial folds, nor in the secretion of the calcareous septa, was there any simulation of a cyclic mode of development. Both mesenteries and septa arose progressively, and the apparent arrangement of these and the tentacles into successively younger orders arose in consequence of predetermined limitations in the extent of their growth.

The development of the mesenteries and the formation of the calcareous parts, as determined by Lacaze-Duthiers, may be briefly outlined as follows: The first differentiation of the visceral cavity of the embryo takes place with the formation of two oppositely placed mesenterial folds, which divide the cavity into two unequal sectors. In the larger of these sectors two new mesenteries arise and divide it into three compartments; shortly thereafter the smaller sector is similarly subdivided by a pair of mesenteries. This alternate insertion of pairs of mesenteries continues until the total number possessed by the animal is achieved, regardless of how large this number may be.

The first deposits of calcite appear when the mesenteries have divided the visceral cavity into twelve compartments. The secretion of calcite takes place within the inner wall, the endoderm or endothelium. The septa are

the first parts to be so formed, and their genesis takes place nearly simultaneously in each of the twelve triangular compartments formed by the junction of two mesenteries with the wall. The deposition of calcite nodules or scleres arises from three centers of secretion in each compartment, one such center being located in each corner of the triangle. With continued growth the two peripheral deposits elongate toward the central one, which advances to meet them, until with their conjunction a Y- or V-shaped arrangement is produced. (Fig. 3). It is not until the formation of the septa is well advanced that the calcification of the wall and base of the coral begins, and when this has progressed sufficiently, the two arms of the septal V coalesce with the wall. The development of a columella does not begin until after the septa have reached this stage.

As the deposition of calcite continues, six alternate septa continue to be enlarged for a considerable time after the other six have reached their full dvelopment, and the difference in size thus produced leads to the appearance of two cycles of septa, of unequal size.

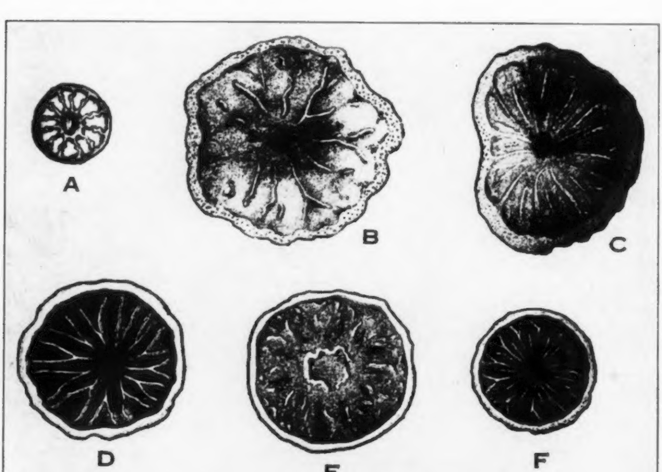


Fig. 3. Some early stages in the formation of the calcareous septa in *Asteroides calycularis*. (After Lacaze-Duthiers).

The stages of development outlined in the foregoing are those observed by Lacaze-Duthiers in the Mediterranean coral, *Asteroides calycularis*, and verified by him upon a number of other forms. It is unfortunate that he was unable to make precise observations beyond the stage in which twelve septa were developed, but his results are none the less significant.

Dybowski's Classification

Concurently with the morphological studies of Kunth and Lacaze-Duthiers two writers of northern Europe were making important contributions to taxonomic and phylogenetic knowledge. Lindström, in Sweden, was already recognized as an authority of fossil corals, although he had not yet published his researches upon the operculated corals, which climaxed his works, and which will be discussed later; and Dybowski, in 1874, published his monograph on the Silurian corals of the Baltic Provinces of Russia.

Dybowski studied corals by means of vertical and transverse thin sections, and he was the first to announce a verification of Kunth's law. While the greater part of his monograph is devoted to the description of new genera and species, its principal importance lies in the presentation of an advancement in the classification of the tetracorals. Dybowski perceived that the entire group Tetracoralla could be divided morphologically into two families, which he named *Inexpleta* and *Expleta*. The two families are very unequal in the number of forms they embrace, the *Inexpleta* being a rather modest group numerically, characterized by the general absence of endothecal structures, while the *Expleta,* which are defined by the existence of tabulae and dissepimental tissue, include the majority of the tetracorals. The advantages of this classification, aside from the fact that the morphology of the forms demands it, is in the analogy it presents with the Hexacoralla, whose principal systematic subdivisions are likewise based upon the nature of the endothecal structures. A further interesting fact brought to light by this grouping is the marked parallelism existing between the *Expleta* and the *Inexpleta,* in consequence of which individual subdivisions of the former are exactly analogous to those of the latter. Thus the Inexpletan *Cyathaxonidae, Petraiidae,* and *Polycoelia* find their counterparts in the Expletan *Axophyllidae, Zaphrentidae,* and *Cyathophyllidae.*

The broader features of Dybowski's classification have won wide-spread acceptance, and are now in general use; his descriptive and morphological work, however, has frequently been subjected to sharp criticism, especially at the hands of Lindström.

Very shortly after the appearance of Dybowski's monograph still further revision of the existing classification of corals was urged by M. G. Dollfus, in a paper read before the Academy of Sciences, in Paris. (1875). Dollfus suggested the division of the *Rugosa* into two classes, the first of which should include those Paleozoic corals having an irregular septal system, with the septa always free, and with or without tabulae. (In general the *Zaphrentinae* and *Cyathaxoninae* of Edwards and Haime). The second class would embrace those types having a regular septal system, with the septa arranged in variable fashions. Since Dollfus argued for the abandonment of the tetrameral character of grouping the septa, the members of his second class would be distinguished from the *Zoantharia aporosa* only by the presence of tabulae. Dollfus lamented the fact that the group *Tabulata* had become merely a dumping ground for poorly known forms; and, in urging its revision, he

presented a series of phylogenetic relationships which he believed could be traced between the tabulates and modern forms. Briefly, the relationships he suggested are:

The Heliolitidae *(Lyellia, Propora)*, are the ancient representatives of the modern millipores, through the intermediation of the Pocilliporidae *(Pocillipora, Axopora, Polytremacis)*.

The Syringoporidae *(Syringopora, Fletcheria, Halysites,* etc.), correspond either to certain Bryozoa *(Hypothoa, Idmonea)*, or to certain tubulose Alcyonaria.

The Chaetetidae with perforate walls *(Stillipora, Chaetetes, Dania, Beaumontia, Labechia, Dekaya)* offer a direct parentage to the Jurassic Bryozoans of the group *Heteropora,* and to the Cretaceous Bryozoa *Radiopora.*

The Favositidae are directly ancestral to the tubulose Bryozoa *(Cyclostomata)*, and the *Dendroporidae* have a similar relationship to the Bryozoa of the group *Hornera.*

Dollfus was content to offer merely criticism and suggestion, and made no effort to set up a detailed classification.

Work of Thomson and Nicholson

Meanwhile, in England, J. Thomson and H. A. Nicholson, the heritors of the extensive material resulting from the five years of study by the British Association's committee on Carboniferous corals, began the publication of their results from the study of this material. The first of these papers was by Nicholson, (1875), and in it he recognized the following modes of growth among Paleozoic corals:

A. *Simple calicular gemmation,* in which the corallum sends up from its calicular disc a single bud, which usually repeats the process, until there is produced a succession of corallites vertically superimposed. This mode is peculiar in that the same calice never produces more than a single bud.

B. *Compound calicular gemmation.* Two or more buds are thrown up from the primitive oral disc, and these commonly repeat the process in turn, until the corallum forms an inverted pyramidal mass, composed of numerous corallites diverging from the base.

C. *Parietal or lateral gemmation.* The corallum increases by the production of buds at some point in the walls of the parent corallite between the lip of the calice and the base.

D. *Basal or marginal gemmation.* New corallites are produced at the circumference of the colony, or along certain definite lines proceeding from the base.

E. *Fission.* The growth of the corallum is effected by the cleavage of the calice of the original corallite or corallites.

Nicholson concluded that little stress could be placed on mode of growth as applied to the classification of Paelozoic corals. He found that allied forms of the same genus, and even different individuals in the same species, show entirely different modes of growth. On the other hand forms belong-

ing to the most remotely related groups often increase in the same way. The common difficulty in recognizing the mode of growth in any particular specimen is a further barrier to the use of this characteristic for classificatory purposes.

The most important fruits of Nicholson's and Thomson's studies appear in a series of papers published during the year 1875. These deal with the recognition of the principal generic types of Paleozoic corals. (Nicholson, 1875a, Thomson and Nicholson, 1875). After stressing the use of serial thin sections as the only possible scientific method for the study of corals, the authors urge, as a basis for classification, the adoption of elastic generic types, rather than a continuance of efforts to isolate genera by rigid definitions. Since Thomson and Nicholson were in possession of unusually abundant data, their argument in favor of generic types is proportionally important, and is here given:

> "As investigated by the method which we have employed, the corals of the Paleozoic period very strongly support the view that they owe their structural peculiarities to some form or another of evolution. Whenever a sufficiently large number of specimens of any given group can be obtained and submitted to examination by means of sections, a complete passage is usually found to exist into other allied groups. So complete is this transition, and so gradual are the steps by which it is effected, that it becomes impossible for the most painstaking observer to draw any hard and fast line of demarcation between such inosculating groups." (Nicholson, 1875a, p. 307).

In keeping with the conclusion thus expressed, Thomson and Nicholson undertook the description of a number of such generic types, giving complete descriptions of the external and internal characters and the relationships of the forms selected. Included as type genera are *Amplexus, Zaphrentis, Cyathophyllum, Campophyllum, Diphyphllum, Lophophyllum, Lithostrotion, Koninckophyllum, Lonsdalia, Clisiophyllum, Dibunophyllum*, and *Aspidophyllum*.

Among the many important contributions to the paleontology of corals appearing in the year 1875 must also be included the description of the Mesozoic corals of the Nattheimer strata, by Becker and Milasewitch. (1875). This lengthy work is primarily of value for the new material which it brings to light, for aside from a discussion of classification, it contains little of a general nature.

Hall and Rominger

The appearance, in 1876, of Carl Rominger's description of the fossil corals of Michigan marks the first important contribution from North America. (1876). During the same year James Hall published his illustrations of the Devonian corals of New York State. Rominger's work contains both descriptions and illustrations, whereas that of Hall is little more than a compilation of plates. In the manner in which they handle their material the American authors are quite antiquated. They are apparently unaware of much of the work which has been done in Europe prior to their publications, and Rominger's descriptions are modelled after those of Edwards and Haime, rather than Thomson and Nicholson. Neither work exhibits any attempt to

use thin seections, either in the ilustrations or in the actual study of the material. The importance of these volumes rests almost entirely on the depiction of new genera and species, as both pioneer into the hinterland of hitherto scarcely touched North American material.

Morphology of G. von Koch

In 1879 G. von Koch published in Germany the first of an important series of morphological papers containing the results of his observations upon both reef and cup corals. In this paper he concluded that the *theca* or wall of the corallum arose from a thickening and fusion of the distal ends of the septa, and not, as had been previously supposed, from a continuation of the foot secretion responsible for the calcification of the base. Von Koch availed himself of the most scientific methods of research known to his time; and in addition to the use of serial thin sections, he introduced an innovation in the use of trasmitted light as a means of detecting variations in the mode of deposition of the calcitic sclerites and nodules revealed in his sections. With the help of this latter tool von Koch analyzed coral skeletons, and classified them as follows: (1882).

A. Skeleton formed of minute free spicules.
   1. Individual corals *(Alcyonaria)*.
B. Skeleton formed partly of fused spicules and partly of crystalline material.
   1. Corals with compound skeletons.
      a. Skeleton secreted by individual polyps; theca formed from the cementing materials of the body; never possess eight true septa. *(Tubipora* and probably *Heliopora,* most *Tabulata)*.
      b. Theca an independent structure; true septa present. (Most recent *Madreporaria perforata* and *aporosa)*.
   2. Individual polyps united by a coenenchymal tissue.
      a. Colonial forms with skeletons composed of fused spicules. *(Corallium, Mopsia,* etc. No fossil forms).
      b. Forms possessing a horny or more or less calcified skeleton secreted by the ectoderm of the coenenchyma. *(Gorgonides, Pennatulides. Isis* is the only known fossil form).

The most important of von Koch's papers, however, appeared in 1883, and dealt with his observations of sexless reproductive methods among Paleozoic corals. (1883). Although his results seem in general to conform with those of Nicholson's earlier study, previously discussed, the work of von Koch is much more precise, and permits a much clearer conception of the successive morphological changes involvel in the formation of young corallites from the parent calyx. As classified by von Koch, a-sexual reproductive methods of Paelozoic corals fall into two general groups, which he names *Internal Budding* and *External Budding*. Under the first of these he includes the following types:

A. *Fission budding.* The wall and endothecal apparatus of the mother calyx are directly transitional to the daughter calyx, without any alteration. The separation of the two results simply from a fusion of the two oppositely lying points of the calicular wall of the parent. (Fig. 4, a).

B. *Septal budding.* The parent calyx becomes subdivided into two or three, or rarely four, buds. A part of the original wall and its septa are transitional to the bud, but an essential part of the wall of the bud is formed from an envelopmental curving of the four primary septa. (Fig. 4, b). This type of reproduction is found in the genus *Stauria.*

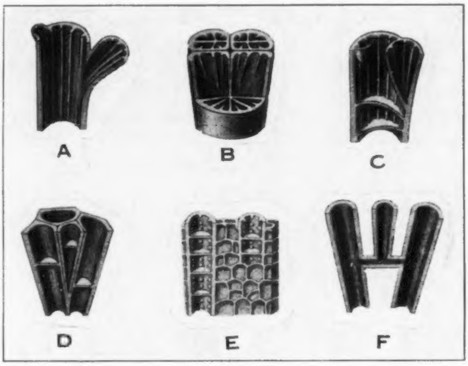


Fig. 4. A sexual reproductive forms. (After von Koch). (a) fission budding. (b) septal budding. (c) tabular budding. (d) interstitial budding. (e) coenenchymal budding. (f) stolon budding.

C. *Tabular budding.* In this type of reproduction the young calyx originates partially from the wall of the one already existing, and becomes completed through a pocket-like bending of a tabula. *Acervularia, Fascicularia, Amplexus,* and *Pholidiphyllum* exhibit this method. (Fig. 4, c).

D. *Interstitial budding.* The mother calyx takes no visible part in the formation of the bud, which appears entirely independently in the interstices between the older calices. *Favosites* and related genera demonstrate this form of increase. (Fig. 4, d).

E. *Coenenchymal budding.* This form of budding is similar to the interstitial budding of the Favosites, except that in it the new calyx arises in the coenenchymal tissue. The bud may be more or less of a continuation of preexisting lamellae in the coenenchyma, or it may be an entirely new structure. This form of budding is shown by *Heliolites,* the modern *Heliopora, Plasmopora, Galaxia,* and analogous forms. (Fig. 4, e).

F. *Stolon budding.* The visceral cavities of the individual corallites are

connected by a tube or stolon. The new bud is formed by the continuation of the walls of the stolon as walls of the infant calyx. (Fig. 4, f). *Syringopora, Syringophyllum,* and the modern genus *Tubipora* exhibit this type of budding.

In addition, von Koch recognized a reproductive form which he termed *rejuvenation,* in which the new calyx is identical with the old one, which becomes constricted and reduced in size, but does not alter otherwise.

Zittel

The year 1879 is made noteworthy by the appearance of Karl A. von Zittel's *Handbuch der Paläontologie.* This work has since become so widely known as a standard reference text for general Paleontology that it is hardly necessary to give here more than a brief notice of Zittel's treatment of corals. The essential purpose of the writer was systematic classification, and his grouping of the corals is a synthesis of what he considered the better features of the existing classifications. Thus, his order *Zoantharia* and sub-order *Madreporaria* are taken from the classification of Milne-Edwards and Haime, but in placing under this sub-order the groups *Tetracoralla* and *Hexacoralla* he follows Haeckel. In subdividing the tetracorals he chose Dybowski's families *Expleta* and *Inexpleta,* and he followed Dybowski further in partitioning the latter family into the sub-families *Diaphragmatora, Plenophora,* and *Cystophora.*

Zittel's classification of the hexacorals is similarly composite, the majority of the divisions being adopted from the work of Milne-Edwards and Haime. In his treatment of the tabulates, he is most revolutionary, however, for he entirely abolishes the group, and disposes of its members in a variety of ways. *Millepora,* and allied forms, and *Labechia,* are placed in the *Hydrozoa;* the entire family of the *Favositidae* is assigned to the hexacorals as a subdivision of the *Poritidae;* a second sub-family of the *Poritidae* is formed by *Koninckophyllum* and *Alveopora; Syringopora, Aulopora, Halysites,* and their relatives are placed in the *Alcyonaria,* in the family Tubiporidae. The *Chaetetidae* are entirely removed from the *Anthozoa,* and placed in the *Bryozoa* under the order *Cyclostomata.*

Very shortly after the publication of the Handbuch, Zittel's dispersal of the tabulates received strong support from H. A. Nicholson in a book devoted entirely to a discussion of the *Tabulata.* (1879). In this work Nicholson corroborated the views of Verril and Lindström as to the necessity of abolishing the *Tabulata* as a distinct and separate subdivision of the *Zoantharia,* and concluded that under the old name "Tabulata" there are included at least twelve distinct groups of corals. For the purpose of his book, however, he retains the tabulates as a unit, and discusses them under the families *Favositidae, Columnaridae, Syringoporidae, Auloporidae, Halysitidae,* (and *Tetradiidae*) *Thecidae* (and *Helioporidae*), *Chaetetidae, Monticuliporidae,* and *Labechidae.*

Nicholson further augmented his studies of the tabulates by publishing, in 1881, a treatise devoted entirely to the genus *Monticulipora.* The avowed

purpose of this lengthy quarto volume is not so much to determine the systematic position of *Monticulipora* as to describe and figure the genus in such detail that its species might always be readily and accurately determined. The incentive to the work was given by Nicholson's disgust with correlations of strata made over wide areas on the basis of species whose determination from the existing descriptions he considered impossible.

An important contribution to the knowledge of modern corals was made in 1880, when C. B. Klunzinger, a German physician and naturalist who lived for many years on the shores of the Red Sea, published his observations of the coralline forms of that region. In his three volume work he suggests many changes in the classification of Milne-Edwards and Haime, and gives in addition a valuable series of photographic plates. (1877-1879).

The return of the Challanger expedition, in 1880, brought even greater additions to the data on modern corals. H. N. Moseley, in his report on the zoological studies of the expedition, verified Dana's contention that the affinities of the Millepores were with the Hydrozoa, and thus finally removed this group from that of the corals proper. (1881). Moseley also devoted a great deal of study to the modern genus *Heliopora*, and he concluded that the fossil genus *Heliolites* is transitional between the present-day *Helioporidae* and some such ancient form as *Favosites forbesi*. In this he directly contradicted the previously mentioned postulation of Dolfuss.

Lindstroem

Gustave Lindström, of Sweden, whose position of authority in regard to the Paleontology of corals has already been noted, published in 1882 his extremely important treatise on the operculated corals. This paper, which is characterized by its thoroughness, is an inclusive discussion of the *Operculata*, tracing the genesis, relationships, and mutations of the group. Lindström divides the operculates into two families, the *Calceolidae* and the *Araeopomatidae*, the former containing the genera *Goniophyllum*, *Platyphyllum*, *Rhizophyllum* and *Calceola*, and the latter the genera *Areopoma* and *Rhipidophyllum*. He sees as the immediate ancestor of the group a mutation of *Goniophyllum pyrimidale*, found at the base of the upper Silurian. Near the close of the late Silurian the group has reached its maximum expansion, and is represented by all of its genera except *Calcola*. In the early Devonian the genus *Rhizophyllum* is the only representative of the group, and *Calceola* of the late Devonian is considered its direct descendant.

Structural Studies of Pratz and Frech

Another important paper appearing in the year 1882 was that of E. Pratz, who studied the septal structure of a number of hexacoral genera, and endeavored to group and relate their forms on the basis of peculiarities in their septal structure. Pratz confined his researches to the fossil members of the *Fungidae*, and he was able to divide the family into four groups, each of which showed distinctive types of septal apparatus. As identifying characters, he used the manner of deposition of the sclerenchymatic substance, the arrangement of the trabiculae, and the presence or absence of synapticulae and

endothecal traverses. He showed that traverses could not be considered as morphological substitutes for synapticulae, since both occurred in the same specimen at times, and he attempted to distinguish between true synapticulae and pseudo-synapticulae, the latter of which he explained as resulting from the union of two trabiculae.

In 1885, Frederich Frech, also a German, published the first of several papers dealing with the middle and upper Devonian corals of Germany. The bulk of Frech's work is devoted to the systematic description of genera and species, (1885, 1886), but one paper is given entirely to a consideration of the skeletal structure and relationship of the tetracorals. (1885a).

In analyzing the structure of the septa, Frech reviews the positions of Dybowski and Kunth, who held that the septa of tetracorals were composed of two parallel lamellae, and that of Lindström, who maintained that but a single lamella was involved in each septum. To this Frech adds his own observation on *Streptelasma,* in which he finds the septa to be formed from infoldings of the outer wall of the corallum. He concludes that each of these three types of structure, and many intermediate modifications of them, may be found among corals of different genera; and that the most common type of septal structure among Paleozoic tetracorals is that depicted by von Koch, in which the septum proper is but a shadowy blade, completely covered by deposits of structureless calcareous material which he named *stereoplasma.*

In regard to the theca, or inner wall of the corallum, Frech finds that ontogenetically and histologically it seems to be composed of the same elements as the septa; in many cases merging with the stereoplasma of the septa without any visible line of demarcation. He concludes from this that the outer wall of the corallum in tetracorals is the theca, and objects to the prevailing use of the term "epitheca" to designate it.

After comparing the skeletal structure of the tetracorals and the hexacorals, Frech says:

> "On zoological grounds it is scarcely possible to rebuff the conception that the *Tetracoralla* may have been the stem ancestors of the *Hexacoralla.* Their geological appearance speaks also for this hypothesis. The 'recoining' appears to have taken place during the period in which the Bunter sandstones were formed. The few Permian forms still belong decidedly to the tetracorals, whereas the genera known from the Muschelkalk and the Alpine Triassic are related to living forms, although, to be sure, the hexacorals still have a somewhat ancient stamp." (1885a, Writer's translation, p. 942).

In 1885 P. Martin Duncan undertook the first important revision of the *Madreporaria (Zoantharia Sclerodermata)* since their classification by Milne-Edwards and Haime. Duncan confined his attention to the broader subdivisions, and excepted the *Rugosa* from consideration. (1885). His suggested revision is as follows:

Order *Madreporaria*
Sub-order *Aporosa*
Family I. *Oculinidae*
II. *Pocilliporidae*
III. *Astraeidae*
IV. *Turbinolidae*
Sub-order *Fungida*

Family I. *Pleisiofungidae*
II. *Fungidae*
III. *Lophoseridae*
IV. *Anabaciadae*
V. *Plesioporitidae*
Sub-order *Perforata*
Family I. *Eupsammidae*
II. *Madreporidae*
III. *Poritidae*

Duncan abolished the sub-order *Tubulosa* of Edwards and Haime, in the belief that its members are not true corals. The sub-order *Tabulata* (E. & H.) is likewise broken up and its members distributed.

The enduring work of Thomson and Nicholson, in England, was continued in 1883 with the appearance of a paper by Thomson dealing with the corals of the Carboniferous of Scotland. (1883). Thomson's object was to illustrate the evolution and close interrelationships of the genera and species he studied, and in a number of respects his paper is revolutionary. For example, under the heading *Hydrozoa* he unites such presumably diverse genera as *Aulopora, Michelinea, Chaetetes, Zaphrentis, Amplexus, Favosites, Syringopora,* etc. As *Zoantharia rugosa* he groups *Diphyphyllum, Lithostrotion, Cyathophyllum, Lonsdalia,* and others, and in *Actinozoa rugosa* are placed *Cyathaxonia, Lophophyllum, Axophyllum, Aulophyllum,* etc.

Thomson chooses the simple and structureless genus *Aulopora* as a starting point for his attempt to trace the interrelationships which he believes must exist in all the genera studied, as a consequence of their evolutionary development. The first developmental step from *Aulopora* is *Cladochonus,* which is likewise nearly structureless, but which has a thin zone of vesicular tissue around its inner wall, and in this Thomson sees a transitional character toward *Syringopora.* The tabulae of *Syringopora* are considered as foreshadowing *Michelinia,* while its peripheral vesicular zone is seen as a forerunner of the broad vesicular zone of *Thysanophyllum.*

In a similar way all the species of the Scottish coral genera are analyzed on the basis of their structural changes, the final result being an evolutionary linking of all the species studied. In many cases the transitions postulated seem clear and probable, but in others the gaps are not so easily bridged, and the work is abundantly open to the criticism of future observers.

Of some importance to morphology is E. von Marenzeller's study of the genus *Flabellum,* published in 1887. In this work is found the first careful observation of the phenomenon now generally known as "septal acceleration." Marenzeller noted that in some species of *Flabellum* the interseptal chambers at either end of the long axis of the corallum seemed especially favored for the addition of new septa, and septa of a higher order appeared here before those of the next lower order had been formed in the other chambers. He also observed that in every species the evolution of septa of the higher orders proceeds irregularly, and that the septa of the first three orders tend to become equal in size through the continued growth of the later ones. Marenzeller was able to divide the genus *Flabellum* into three major groups on the basis

of the number of septa in a cycle, and the rate and ratio in which these were inserted.

Concurrently with the above-mentioned work of Marenzellar, G. von Koch published another of his important morphological studies. (1886). In this he discusses the coral skeleton in its relation to the soft parts of the body. Of particular importance are his subdivisions of the skeleton, which are here given:

I. *The Basal Plate.* This separates the arboreal end-surface of the soft body from the underlying surface which holds the skeleton erect. Its form is to a high degree dependent upon the form of the supporting surface, but in general it may be said to be flat and circular.

II. *The Outer Plate.* (Epitheca). A continuation of the basal plate, more or less distinctly set off from the latter, and covering the body wall upon the outside. Among most corals the outer plate is conical in shape.

III. *The Inner Plate.* (Theca). This has generally a ring shape, and projects upward from the basal plate parallel to the soft body walls, becoming covered by in-foldings of these latter. Since many such folds may be laid on concentrically, there may thus be a number of inner plates in a given individual.

IV. *Radial Plates.* (Septa). These plates form radial walls rising vertically from the basal plate, and lying within radial folds of the body wall. They exist in the majority of corals.

William Waagen, as part of his many years of study of the invertebrate forms of the Salt Range of India, published in 1886 and 1887 his description of the corals of the Productus limestone of that region. He devoted the greater part of his large volume to the descriptions of new genera and species from this hitherto little known area, but in a number of cases he attempted to bring his material to bear on the solution of morphological or phylogenetic questions then in dispute. The most important effort of this kind occurs in his study of the genus *Monticulipora,* in regard to which Waagen sided with Nicholson, holding it to be a coral, as opposed to Lindström and Rominger, who considered it a *Bryozoan.* As a basis for his point of view, Waagen offered his discovery of a type of gemmation peculiar to the *Monticuliporidae,* which he named "Intramural Gemmation." In this mode of growth the new corallite is produced by a splitting of the primary mural plates of two or more adjacent corallites, which first become thickened, and then divide in half to furnish the walls of the new bud.

Waagen found that tetracorals are very sparsely represented in the Productus limestone, but that hexacorals of the tabulate type abound. He considered the Paleozoic age of the hexacorals to be conclusively proved by the relationship of the *Favositidae* to the *Poritidae.*

Neumayr

In 1869 there appeared the first volume of M. Neumayr's "Stämme des Thierreichs," a work probably of more importance to general Paleontology than any since the publication of Zittel's "Handbuch." Unlike Zittel, Neumayr did not aim at systematic classification, but attempted rather a

general survey and review of all the existing data respecting fossil invertebrates, endeavoring to depict their origins, developments, relationships, and trends.

In his discussion of the corals, Neumayr found little difficulty in linking the Mesozoic and Tertiary forms with the modern representatives of the group, but he was forced to leave the tetracorals in a somewhat uncertain position; we can perhaps do no better than consider his own words in this regard:

"Let us cast a backward glance over the entire field of the tetracorals which are provided with endothecal structures, and we thus find that the *Cyathophyllidae* form the mid-point, about which all the other families, the *Zaphrentidae*, *Axophyllidae*, *Cystiphyllidae*, and *Calceolidae*, group themselves; while, however, the three last named groups certainly represent strongly differentiated, diverging types, their significantly developed bilaterality makes it probable that the *Zaphrentidae* belong in another position, and show an original structure. *Streptelasma*, in particular, is a form which has been supposed to be the most primitive of the tetracorals known up to the present—an interpretation which is in complete accord with the geologic occurrence of this genus.

"In general, however, our knowledge in this regard is still fairly small, and the tetracoral branch could be put forth from the genealogical tree only with great difficulty, were it not for the remarkable phenomenon that the morphological relationships show a simple, straight line relationship, and not a network of offshoots. In other words, the existing relationships stand in good accord with the requirements of the theory of evolution, and the geologic sequence agrees with the accepted evolution in its general features." (1869, writer's translation, p. 270).

Neumayr believed that the bilaterality and peculiar mode of septal insertion of the tetracorals formed at once their most distinctive characteristic and the most promising clue to their future linkage with other groups.

As an important successor to James Hall in extending the knowledge of North American fossil corals there must be mentioned Amos Worthen, state geologist of Illinois. Like those of Hall, Worthen's labors were mainly confined to the description of new species, his material, however, being drawn from the Mississippian strata of Illinois and the adjacent states. (1889).

A descriptive work of much greater scope is that of P. Pocta, whose treatise on the Silurian corals of Bohemia appeared in 1894, as part of Barrande's "Systeme Silurienne du Centre de la Boheme." Pocta's work is of importance as a reference for the description and figures of a multitude of forms, but he confined himself for the most part to bare description of the external characters of his material.

Phylogeny of Haeckel

In 1896 Ernst Haeckel published the second volume of his "Systematische Phylogenie," As its title indicates, the purpose of the work is two-fold: the systematic classification of living and fossil forms on a morphological basis; and the synthesizing of both into a smoothly branching genealogical tree. Haeckel's attempt is more ambitious than the somewhat similar one of Neumayr, in that the latter confined himself to fossil forms only; and at first glance Haeckel seems to have been much more successful in achieving a connected evolutionary series. To do this, however, he was forced to postulate a considerable number of ancestral and linking groups which have no

known existence other than in the mind of the author. He justified the employment of such groups, however, by asserting that the morphology of known forms necessarily implied the existence of the postulated ones.

The order *Staurocorallia,* with its subdivisions, which Haeckel postulated to complete the evolutionary series of the corals, is typical of his use of hypothetical groups. As the ancestral type of the coral stock, Haeckel imagined a bilaterally symmetrical form exhibiting a fourfold arrangement; one having four tentacles, four major septa, and four visceral loculi. From such an ancient form he believed the later corals with six-fold, eight-fold, or higher symmetries to have been derived.

As a transitional group between the *Tetracoralla* and the *Hexacoralla,* Haeckel selected the *Mesocoralla,* or *Octozoantha,* forms whose tentacles and septa occur in groups of eight, or multiples of eight. The transition he conceived to have taken place through a doubling of the fourfold groups of the tetracorals to produce the eightfold type characteristic of the Mesocorals, and these in turn achieve the twelve septa and tentacles of the Hexacorals by the addition of four lateral ones. In support of this argument he called attention to the ontogeny of the hexacorals, which in the course of their early development go through a stage exactly recapitulating the eightfold symmetry of the members of the Mesocoral family *Edwardsia,* and then later add four more septa to achieve the typical hexacoral structure. In this ontogenetic development of the hexacorals, Haeckel sees proof of their Mesocoral ancestry. The close relationship of the former to the tetracorals, however, lacks any such concrete evidence.

Two other works appearing in the year 1896 warrant mention as important repositories of data on the genera and species of new areas. These are Lindström's description of the upper Silurian corals of the island of Gothland, and A. Stuckenburg's report on the Carboniferous corals of the Ural and Timan regions of Russia. The former is a model of careful analysis and description, with some attempts to place the forms studied phylogenetically. The latter is a much more general description of the coral fauna of a region hitherto almost unknown, and brings to light 136 new species of tetracorals and tabulates.

Morphology of Marie Ogilvie

In 1897 Marie Ogilvie, a student of von Zittel, attempted a most ambitious revision of the entire order Madreporaria. (1897a). The foundation of her work is a detailed microscopic study of the skeleton, analyzing the mode of growth, the relationships, and the evolutionary history of the component parts.

Miss Ogilvie found the Madreporarian skeleton to be built up of successive calcareous growth laminae, similar to those of mollusc shells. The fundamental unit of structure is the *caliculoblast,* an ectodermal cell in which, by a process of chemical change, lime is secreted and at once laid down within the cell in the form of aragonite fibres. Each lamina is alternately banded with a narrow zone, dark by transmitted light, and a broader, lighter, crystalline band. The former represent the proximal organic ends of the cali-

culoblasta, and the latter the fibrous deposits of the adjacent cells. These bands are less readily distinguished in progressively older forms.

After an exhaustive examination of the skeletal structures of representative genera of each living coral family, Miss Gordon attempted to trace peculiarities of structure backward through the genera of fossils, and to isolate phylogenetic groups on the basis of structural homologies and differences. She concluded that the evolution of the Madreporaria has proceeded without interruption from Paelozoic to modern forms, the transition from ancient to recent types taking place most pronouncedly in the Triassic and Jurassic periods. The many branches of the living Madreporaria spring mainly from two trunks, the *Madreporaria Haplophracta (Zaphrentoidea)*, and the *Madreporaria Pollophracta (Cyathophylloidea.)* The one is characterized as a primitive group, slow to advance, and prone to retrogress, while the other has always been in the forefront of evolutionary advance, quick to adapt, and seldom retrograde.

In some contrast to Miss Ogilvie's work is the grouping of the corals put forth by W. Volz as a conclusion to his description of the corals of the St. Cassian strata, in 1897. Volz' classification attempts to be both historical and phylogenetic. He divides the corals into four groups:

I. The *Archeocyathidae* of the cambrian.

II. A Silurian and Devonian division, characterized by the families *Operculata, Cyathophyllidae, Cyathaxonidae, Paleocyclidae* and *Cystiphyllidae;* and a Carboniferous and Permian division in which most of the preceding genera show a pinnate septal arrangement.

III. A transition group introduced at the close of the Paleozoic, and marked by a mixing of ancient and modern forms. The *Styllophyllidae* and *Pinnacophyllidae,* both belonging to the Zaphrentoid stem, are most characteristic of this division. Of even greater significance for the evolution of later forms is the splitting of the *Cyathophyllidae* into the *Astraeidae* and *Thamnastraidae,* which is completed at the beginning of this period.

IV. The last evolutionary division of the corals is introduced during the middle Lias, and is characterized by a dominating trend in the direction of modern forms. At the outset of this group the *Astraeidae* and *Thamnastraeidae* are its most numerous forms.

Early Work of Weissermel

Yet another addition to phylogenetic theory was made in 1897 by W. Weissermel, in connection with his studies on the genus *Columnaria.* His ideas on the evolutionary stock of the corals may be readily interpreted from figure 5.

Weissermel also offered a suggestion as to the origin of the bilateral symmetry of solitary tetracorals. Postulating the existence of the coral cup on the sea bottom under conditions in which nutritive material was brought within range of the tentacles by a current streaming in a definite direction, he concluded that the polyp would tend to bend in the direction of the current, in order to present the greatest tentacular and oral area toward the supply of

food. From this would arise the characteristic cornute shape of the tetracoral corallum, and further, by virtue of its more favorable situation, the upper half of the calyx would tend to receive more nourishment than the lower, and in consequence would grow more rapidly and extensively. The bilateral symmetry of the tetracorals would thus be a consequence of this differential growth of the upper half of the calyx.

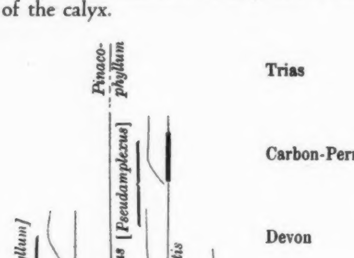


Fig. 5. Phylogeny of the Tetracorals according to Weissermel.

Structural Units of G. C. Bourne

The conception of the caliculoblast cell as the elemental structural unit of the coralline skeleton, an idea originating with von Heider, and elaborated by Miss Ogilvie, was strongly criticized by G. C. Bourne in a paper dealing with the structure of the Anthozoan skeleton, published in 1899. After a study of spicule formation in the *Alcyonaria,* and of the skeleton in *Heliopora* and a number of *Madreporaria,* Bourne concluded, as had von Koch, that the basic unit of the Anthozoan skeleton is a minute nodule or spheroid of calcium carbonate. These calcareous particles, according to Bourne, crystallize out of an organic liquid matrix secreted by the caliculoblast layer, and attach themselves to the pre-existing crystalline structures in such a way as to preserve the shape and orientation of the latter, exactly as in the growth of a crystal. The entire process of skeletal formation is analogous to the development of a crystal, and subject to the same laws, but in some manner, as yet unexplained, the general arrangement of the fasciculi of crystals is dominated by the living tissues which clothe the corallum.

Ontogeny of J. E. Duerden

Almost since the inception of their study, the primitive tetrameral symmetry of the *Rugosa* had been accepted as practically self-evident by the ma-

jority of workers, and this idea appeared to be abundantly confirmed by the discoveries of Kunth. The only noteworthy exceptions to this view were those of Ludwig and Pourtales, each of whom claimed to have observed six initial septa in the very earliest stages of certain tetracorals. The theory of a fundamental and primitive hexameral symmetry in Paleozoic corals was strongly championed by J. E. Duerden, in an extensive series of papers dating from 1900. As a result of grinding down the tips of a number of individuals of *Lophophyllum proliferum,* and examining the structure thus revealed in the earliest formed portion of the corallum, Duerden was able to confirm Pourtales' observation that this coral has six primary septa (protosepta), situated equal distances apart, and that new septa were added bilaterally in four of the six primary interseptal chambers, that is, in the two middle and the two ventro-lateral chambers. He observed further that the addition of new septa took place at only one region within each chamber—"immediately dorsal to the alar or vetro-lateral septum in the case of the middle chambers, and immediately next to the cardinal or ventral directive septum in the ventro-lateral chambers." (1906, p. 227).

By comparing the septa of fossil corals with the mesenteries of living ones, Duerden concluded that the *Zoantheae* are the closest living relatives of the *Rugosa,* for in the former the secondary mesenteries (metacnemes) are added bilaterally at one region within each of the primary ventro-lateral intermesenterial chambers, exactly as are the septa in the tetracorals.

From a study of the structure and development of the fossula in *Streptelasma rectum* Duerden derived further evidence favoring his theory that the *Zoantheae* and the *Rugosa* are closely related. He observed that the fossula in *Streptelasma rectum* is made up of a series of incomplete septa on either side of the cardinal septum, which is itself smaller than the other primary septa. This suggested to him that the atrophication of the cardinal septum could be correlated with the presence of a ventral gonidial groove similar to that of modern zoanthids.

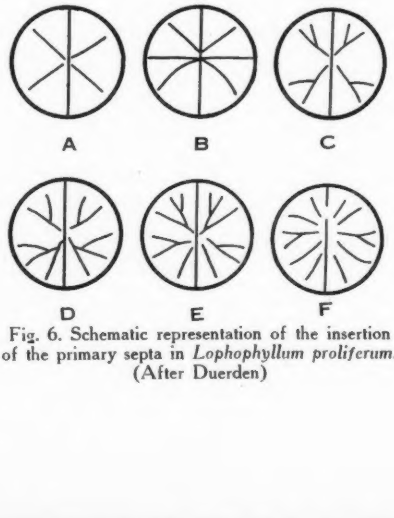


Fig. 6. Schematic representation of the insertion of the primary septa in *Lophophyllum proliferum.* (After Duerden)

Very shortly after its complete formulation, Duerden's theory was strongly criticized by C. E. Gordon, who affirmed that he had studied five or six young specimens of *Lophophyllum proliferum,* and in every case had found four primary septa extending farther into the tip than any other septa. Gordon explained the appearance of six primary septa observed by Duerden as being probably due to septal acceleration, whereby a pair of secondary septa, through premature development, simulated primary septa. (1906).

To this criticism Duerden replied at once, not only re-affirming his original conclusions, but listing four additional species in which he claimed to have discovered unmistakeable evidence of six primary septa. These species were *Cyathaxonia cynodon, Streptelasma rectum, Zaphrentis pusilla,* and *Duncanella borealis,* and for each of them he published serial sections evidencing a hexameral symmetry in the initial stages of development. (1906b).

Morphological Theories of H. M. Bernard

During the period in which Duerden was thus engaged in developing his theory of a hexameral ancestry for the tetracorals, H. M. Bernard, of England, offered some entirely new concepts of the synthesis of the Madreporarian skeleton. Bernard centered his study around the "prototheca," a tiny saucer-shaped structure which he conceived to be the first step in the development of an individual skeleton or the parent calicle of a colony. According to his definition,

> "This *prototheca* is not a composite structure, but a morphological unit, the rim of which can be bent up, flattened completely down, and indefinitely expanded in any direction as a film, from the upper surface of which, as originally from within the cup, the coral skeleton arises. . . This film is the Epitheca." (1904, p. 4).

In thus concluding the epitheca as part of the prototheca, Bernard differs from von Koch's conception of the "basal plate," since the latter considered the epitheca an independent structure, and described it as the "outer plate."

In the successive formation of protothecid saucers, and their epithecal phases, Bernard felt that he had an important clue to the structure of corals, and he summarized his theory as follows:

> "For an understanding of the morphology of the coral skeleton, we must bear in mind that essentially the same process, viz., *a succession of epithecal cups or saucers, occurs throughout the whole of the Madreporaria.* They may be simple conical cups, fitted one into the other *(Zaphrentis)* or flat plates piled up *(Montlivaltia, Goniopora),* or their epithecal floors may be thrown into complicated folds and both the cup and its repetitions may be difficult to unravel, but the fundamental principle is the same throughout. . . . We repeat then, for the sake of emphasis, that wherever the epitheca occurs it represents the rim, or the coalesced rims, of one or more protothecal cups or saucers, the floors of which are represented by the tabulae. In any individual case the tabula below the living layer is the *n*th repetition of the original prototheca of the parent polyp." (1904, p. 9).

As a supplement to the foregoing theory, Bernard also attempted to explain the shape of the adult corallum in terms of the prototheca. He suggested that cornute solitary corals, such as *Zaphrentis* and *Menophyllum,* owe their horn shape to the falling over of the prototheca, with its gravitative effect on the tissues instituting the septa, later growth into a vertical position

once more giving rise to a secondary radiality. Bernard considered the entire group *Tetracoralla* to be no true division of the corals, but merely an assemblage of forms whose common characteristics of shape and structure were derived from this early falling-over of the prototheca.

In the belief that the shape of the prototheca is a character of diagnostic importance, Bernard devised methods for diagraming it, and attempted to employ such diagrams in tracing phylogenetic relationships. Some idea of his protothecal types, and the manner in which they are combined to produce varied forms of coralla, is given in figure 7.

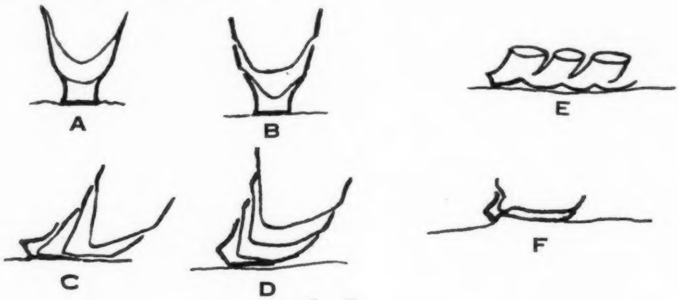


Fig. 7.

a) The three earliest growth periods of a primitive Madreporarian. The thick basal part is the prototheca.

b) Same, regarded hypothetically as three separate cups. (The lowest is the prototheca.)

c) Early stage like (a), but having fallen over and begun upright grow again. Fossula on the convex side.

d) Falling over of a wide-mouthed prototheca. Fossula on the convex side.

e) Method of budding of prone prototheca.

f) One sided bending over of prototheca. (After Bernard).

Ontogenetic Studies of Carruthers

The theory that the *Rugosa* possess six primary septa received strong additional support in a paper published in 1906 by R. G. Carruthers. **(1906)**. For the purpose of definitely settling this much disputed point, Carruthers sectioned the tips of a variety of tetracorals, chiefly Zaphrentids, and worked out the plan of their septal insertion in careful detail. The various stages of the development of the septa, as he observed them, are as follows:

I. A single septum stretches entirely across the calicle, from wall to wall. At a considerably later stage this breaks near the center, the two halves forming the cardinal and counter septa. This first formed septum Carruthers designated as the "axial septum."

II. Two new septa arise, one on either side of the axial septum, at its cardinal end. These remain attached to the wall of the corallum and to the

axial septum, but gradually spread outwards, and eventually become the alar septa.

III. A second pair of septa appear at the counter end of the axial septum, and similarly spread outward, but to a much more limited extent than the first pair.

The disruption of the axial septum completes the formation of six primary septa. Secondary septa are likewise inserted in pairs, arising on the fossular surfaces of the last formed septa, but instead of moving outwards, as did the lateral primaries, they all move toward the counter septum. The entire plan can readily be understood from a study of the appended diagram.

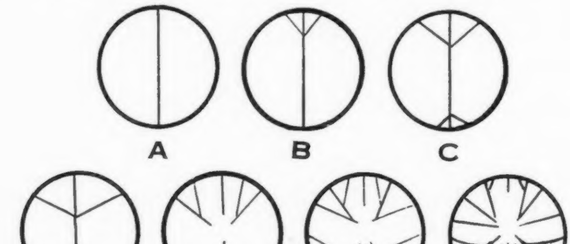


Fig. 8. Diagram showing the development of the protosepta in Tetracorals as observed by Carruthers.

The explanation of septal insertion offered by Carruthers was called into question by T. C. Brown, in a paper published in 1909. After a study of the early stages in the development of *Streptelasma,* a genus also analyzed by Carruthers, Brown found the structure to be exactly as Carruthers had represented, but he disagreed with Carruthers in the manner of interpreting it. Brown suggested that the two counter primaries could be better interpreted as secondary septa. He insisted that failure to so interpret them would involve the necessity of assuming for *Streptelasma* a septal arrangement entirely different from that of any other rugose coral, as the cardinal quadrants would then have one more pair of septa than the counter quadrants.

In 1909 L. Faurot, of France, published the results of his study of the septal development of *Cyathaxonia,* and essentially corroborated the scheme of septal insertion offered by Carruthers. Faurot found that the tetracorals, as represented by Cyathaxonids, have six primary septa, and he verified the existence of a single initial axial septum, as described by Carruthers. His diagram of the first stages of septal development in *Cyathaxonia* differs from the diagram of Carruthers only in minor details.

Faurot's primary purpose, however, was to compare the septal develop-

ment of the *Rugosa* with that of the Hexactinids, Zoanthids, and Cerianthids, to determine the degree of relationship existing between them. He concluded that the Cerianthids are the unique descendants of the tetracorals, for they alone among living corals preserve the primitive disposition of the septa into four groups. (1909a).

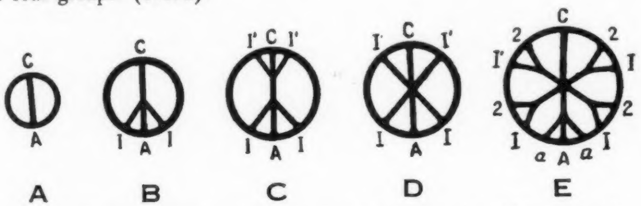


Fig. 9. The development of the protosepta in *Cyathaxonia*. (After Faurot)

An important step in unravelling the complications of the genus *Zaphrentis* was taken by Achille Salée in his revision of the genus, *Caninia*, published in 1910. Salée was able to determine a number of diagnostic characters separating *Zaphrentis* from *Caninia*, and he also simplified taxonomy by showing that the forms described by Milne-Edwards and Haime, and de Koninck, as *Zaphrentis vermicularis*, *Z. Dumonti*, *Z. Nystiana*, *Z. Edwardsiana*, and *Z. cornu-bovis* are actually only successive stages in the development of *Caninia cornucopiae*.

Morphological Theories of Yakowlew

For more than a decade subsequent to 1910, N. N. Yakowlew, of Russia, devoted a series of papers in three languages to an effort to elucidate the origin of the structural peculiarities characterizing the *Rugosa*. As important differences between the *Rugosa* and the *Hexacoralla*, he cited the conical polyparium of the former, as contrasted with the cylindrical one of the latter, and the lateral attachment of the tetracorals, as opposed to the tip attachment of the hexacorals. The habit of lateral attachment evinced by the tetracorals Yakowlew suggested might be correlated with their life in shallow epicontinental waters, subject to agitation from strong currents and large waves; the hexacorals, dwelling in greater depths, had less need for rigid support. Like Weissermel, Yakowlew explained the cornute shape of the tetracoral polyparium as being due to orientation with respect to the prevailing currents, but he exactly opposed Weissermel by holding that the bending was away from the current, to avoid suffocation from sediments, and not toward it to obtain food. (1917a).

With regard to the internal structure of the coral skeleton, Yakowlew believed that the insertion of secondary septa was a function of the conditions imposed by the curved state of the corallum, and the mechanical difficulties entailed by the pre-existence of the primary septa. He observed further that the mouth of a conical polyparium is commonly in a plane perpendicular to the convex side, and that the secondary septa have a tendency to grow in a

plane perepndicular to that of the mouth. The outcome of these conditions is that it is possible for the secondary septa to grow unimpeded, in the manner stated, only in the two counter quadrants. In the cardinal quadrants they are forced to grow in such manner that their outcrops on the wall of the corallum are parallel with those of the alar septa. This structure and its possible variations are shown diagrammatically in figure 10. (1915).

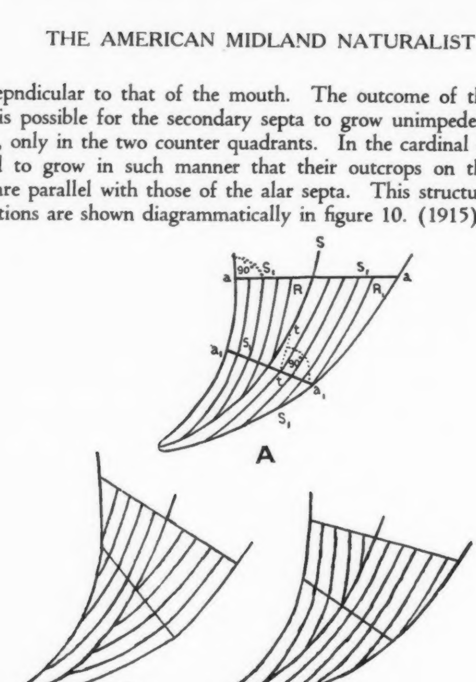


Fig. 10. Diagram showing the outcrops of the septa on the surface of the polyparium, according to whether the mouth is at right angles to the concave side (a), to the convex side (b), or to neither (c).

A good summary of the evidence bearing upon the ancestry of the hexacorals, and their possible relationship to the tetracorals is presented by J. W. Robinson in a paper published in 1917. After considering the alternative possibilities that the *Hexacoralla* are either directly descended from the *Tetracoralla,* or that they existed through the entire Paleozoic as soft-bodied, skeletonless forms, Robinson concludes in favor of the former theory. The principal factor influencing his conclusions is the widespread development of a columella among the tetracorals toward the close of the Paleozoic, for this structure is also found extensively developed among the hexacorals at their inception in the Mesozoic.

The theories of Yakowlew regarding the influence of sessility and lateral attachment in determining the shape of the tetracoral polyparium were seconded by Otto Jaekel in a paper published in 1918. Jaekel, however, felt that it was necessary to consider a still earlier stage of coral ontogeny than had Yakowlew, and to explain those feautres in the structure of a coral which are present at its inception as an individual, and which antedate any possible influence of environment. For this purpose he employed the *Planula* larva of

the *Anthozoa*, a free-swimming, worm-like form. He suggested that at the close of its larval existence, the *Planula* folded upon itself like a U-tube, so as to bring its oral and posterior ends into conjunction, the extremities and ventral surfaces fusing together. This form, he suggested, might represent the initial stage in the existence of a coral, the subsequent structural developments being controlled by the peculiarities of the two halves of the larva. As the principal evidence in favor of his hypothesis, Jaekel pointed out that the corallum of a tetracoral was naturally divided into two unequal and dissimilar portions by a plane passing through the Alar septa. In one such area the septa were inserted in a pinnate fashion, while in the other a radial arrangement prevailed. These differences, according to Jaekel, are to be correlated with the origin of the two areas from the posterior and anterior halves of the larval form, the Alar septa being the reflection of the ventral fusion.

Although of relatively minor scope, it is of some technical importance to note that in keeping with the foregoing work, Jaekel corrected a misconception regarding the position of the *Rugae* or stripes seen upon the external surface of the corallum in a wide variety of tetracoral genera. He showed that these rugae were not continuous in position with the septa, but represented rather the position of the tentacles, and were consequently the external reflection of the interseptal loculi. From this he made it apparent that the Cardinal septum, situated in a fossula composed of two such loculi, will be represented on the external surface of the corallum by two parallel rugae.

Shortly after Jaekel published his theory of Anthozoan structure, A. Krempf, in a report to the Academy of Sciences in Paris, announced that a study of Anthozoan embryos had yielded him unmistakeable evidence of a primitive bilateral symmetry, present in the embryo in the very first hours of its existence, and in this respect differentiating the *Anthozoa* from all other *Cnidaria*. (1919, 1919a).

Theories of W. D. Lang

In 1917 and 1923 W. D. Lang, of England, published two very important discussions dealing with the influence of homeomorphy on the classification of corals, and setting forth the dominant trends which seem to have governed coral evolution. Lang cautioned against too readily refering to the same lineage forms separated by great chronological intervals, even though they appear to show conspicuous similarities of structure. In support of this warning he cited the well known fact that similarity of environment and function tends to bring about similarity of structure. As possible examples of such convergence he suggested the ancient *Heliolites* and the modern *Heliopora*, which are commonly considered to stand in direct genetic relationship to each other, and pointed out that if they are truly of the same lineage, it is strange that not one of the intermediate forms has been preserved in the geological record. A similar condition exists between the ancient *Syringopora* and the modern *Tubipora*, and among numerous other forms.

Of the greatest importance to the formation of homeomorphs in corals, however, Lang considered the existence of certain definite lines of evolution which are persistent in their expression. He defines four such evolutionary

tendencies: (1) Failure to part with the products of fission and budding; such, for example, as produces a *Thecosmilia* from a compound *Montlivaltia*. (2) Increased extension of the corallum resulting from incomplete fission at the distal end, giving meandriform corals. *(Latimeandra, Phyllogyra, Meandrina)*. (3) Communication of the corallites through abolishing separating walls, producing coralla of individuals with confluent septa. *(Thamnastria)*. (4) Perforation of the corallites, resulting in a reduction of the skeleton through the medium of pores. From this arise the numerous modern genera known as the "perforates," such, for example, as *Porites* and *Goniopora*. Fossil examples are *Kobya* and *Microsmilia*. More than any other factors, the expresion of these four tendencies are responsible for the formation of homeomorphs, and efforts to relate the *Tetracoralla* and *Hexacoralla* are apt to be based on homeomorphy rather than true descent. Lang favored the idea that the tetracorals died out at the close of the Paleozoic period, and were replaced by the hexacorals, which arose anew from a soft-bodied ancestor.

After having emphasized the difficulty of recognizing characters which are truly diagnostic of coral genera, Lang attempted the solution of this problem in its application to Carboniferous corals by classifying them in accordance with the type of "trend" which appeared to have governed their development. His discussion is begun with a consideration of the various types of corallum, which he classifies as follows: (1) Haploid—a simple cornute form; (2) Dendroid—a finger-like aggregate of cups; (3) Phaceloid—a bundle of corallites lying approximately parallel; when these are so closely packed together as to become polygonal, they are (4) Cerioid; when the boundaries of the Cerioid forms become indefinite they are (5) Astraeoid; and when the septa of contiguous corallites become confluent, the corallites are (6) Thamnastraeoid.

Lang then makes a survey of the Carboniferous corals, and defines the following trends:

1. *Astraeoid trend*—an evolutionary tendency directed toward the achievement of the Astraeform type of corallite.

2. *Caninoid trend*—a trend in the shape of a single corallite from discoid through trochoid to cylindroid.

3. *Cyathophylloid trend*—a tendency to radial symmetry, with obscuration of the bilateral symmetry through the introduction of secondary septa, reduction of the Cardinal septum, and arrangement of the septa in groups of four.

4. *Amplexoid trend*—evidenced by the distal retreat of the septa.

5. *Lonsdaleoid trend*—evidenced through a proximal retreat of the septa.

6. *Cystiphylloid trend*—shown in the development of dissepiments.

7. *Aulophylloid trend*—a trend toward complexity and irregularity of the central column.

8. *Petraeoid trend*—a secondary thickening through the filling in of space caused by the distal retreat of the septa.

Through the application of the foregoing criteria, Lang was able to divide

the Carboniferous corals into groups which he considered to be truly related genetically. Figure 11 shows typical cross-sections of representative members of each of these groups.

Gerth

In 1919 H. Gerth offered further evidence tending to confirm an initial six-fold symmetry in tetracorals. In a paper devoted to a review of the development of the septal apparatus in ancient and modern corals, Gerth figured thin sections of *Plerophyllum radiciforme*, from the Permian of Timor, which showed both the first and second pairs of Alar septa strongly developed over the Metasepta. The visible existence of a second pair of Alar septa, thus afforded, strongly verifies the six-fold plan of septal development urged by Duerdin and Carruthers. Gerth also pointed out that the succession in the appearance of the first six mesenteries in the young of modern corals is analogous to that of the primary septa of the *Rugosa*. All further septal and mesentery formation in recent corals is as a rule cyclic, and later insertion in certain positions and repression of new structures in others is a consequence of asymmetrical growth of the calyx. Similarly, the metasepta of the *Rugosa* are inserted in four of the six primary interspaces as a consequence of repression and asymmetric growth. Gerth contended that there was no profound structural difference prohibiting a direct relationship between the *Rugosa* and living *Madreporaria*.

Phylogeny of F. W. Sardeson

A unique viewpoint regarding the ancestry of the corals is that published in 1924 by F. W. Sardeson. This writer regards Ordovician corals of the genus *Tetradium* as ancestral to both tetracorals and tabulates. He attempts to show diagrammatically that differential retardation of cell fission in *Tetradium* is the logical preliminary to the formation of the two distinct types of cell found in *Heliolites*, which is thus considered a descendant of *Tetradium*. On the other hand, if the retardation of cell fission in *Tetradium* is carried to the extreme, a form similar to *Streptelasma* may be produced. Sardeson also suggests that Tetradium may be related to the sponges by way of the *Archeocyathids*. The evidence adduced, however, scarcely seems to support the magnitude of his conclusions.

Weissermel

A very fine survey of the similarities and differences of the tetracorals and hexacorals, with a view of deducing their relationships, was given in 1927 by W. Weissermel. In contrasting the two groups, Weissermel emphasized the following points: (1) The tetracorals possess four conspicuous primary septa; the hexacorals have six. (2) Septal insertion in the tetracorals is definitely localized, but in the hexacorals new septa are added over the entire periphery. (3) The tetracorals develop only two cycles of septa, whereas the hexacorals commonly have more than two, although some forms are known which possess septa of only the first and second orders. (4) The hexacorals commonly expand by lateral growth; the general direction of growth of the

tetracorals is upward. (5) The tetracorals almost always have a well developed theca, but among the hexacorals this structure is frequently lacking or much reduced. (6) The tetracorals have the rugae opposite the interseptal spaces; in the hexacorals the rugae are analogous to the septa themselves. (7) A coenenchyma is common among the hexacorals, but it is scarcely known among the tetracorals. (8) The columella is of uncertain significance, but a pseudo-columella is much more common in the tetracorals. (9) The hexacorals have a strong tendency to develop a porous skeleton, a condition rare in tetracorals. (10) The development of synapticulae to support elongated septa is peculiar to the hexacorals. (11) The tetracorals have a tendency to an elongated, tube-like shape, which, when duplicated by the hexacorals, gives rise to form analogous to the tetracorals, as is shown in the tabulae and disseppiments, and the lack of synapticulae exhibited by the *Astraeidae.*

Weissermel suggested that the tabulates arose from the extreme constriction of the calicular diameter caused by energetic vertical growth. The other characteristic tabulate features, such as reduction of septa and strong development of tabulae, follow naturally from such a condition. When a marked reduction of the calicular radius occurs in the hexacorals, the resulting forms are very similar to the tabulates. *(Alveopora, Favositipora, Heliopora).*

After considering the evidence for six Protosepta in the tetracorals, Weissermel concludes in favor of such a condition, and then proceeds to the description of the transition group of forms showing a mixture of both tetracoral and hexacoral characteristics. Foremost among these is the genus *Plerophyllum,* from the Permo-Carboniferous of Australia and Timor, in which there are five well developed Protosepta. Gerth observed that the insertion of septa in *Plerophyllum* was after the orthodox tetracoral fashion except for the development of the third pair of Protosepta. A second transitional form is *Polycoelia profundum,* which displays a disposition to develop more than two cycles of septa, and to suppress the bilateral arrangement. In *Prosmilia cyathophylloides* and *P. angusta* there are five distinct orders of septa. *Pinnacophyllum* and *Omphalophyllia* are Permian genera which have almost lost the differentiation between protosepta and metsepta.

Fig. 11.

A-F Transverse Sections of Carboniferous Corals.
- a. *Zaphrentis*
- b. *Palaeosmilia.*
- c. *Lithostrotion.*
- d. *Lonsdaleia.*
- e. *Amplexus.*
- f. *Caninia* (typical form).

G-I Sections of Central Columns of Clisiophyllid Corals.
- g. *Clisiophyllum.*
- h. *Rhodophyllum.*
- i. *Aulophyllum.*

J-L Sections of Carboniferous Corals.
- j. *Caninia* (advanced stage).
- k. *Cyathaxonia.*
- l. *Carruthersella.*

(After W. D. Lang)

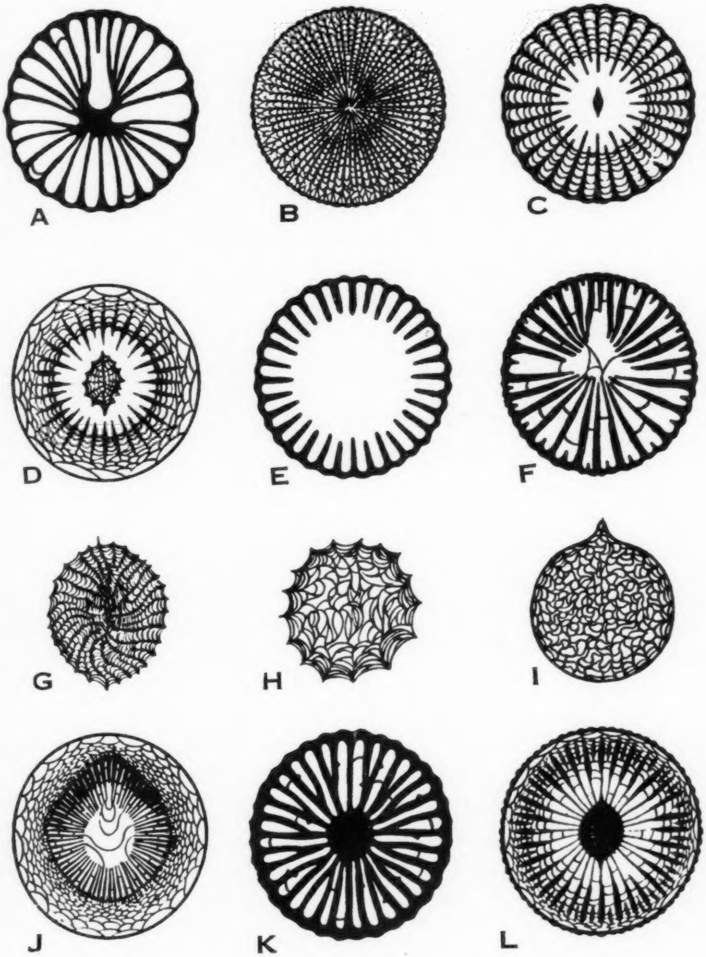
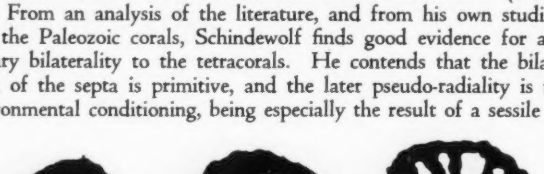


Fig. 11

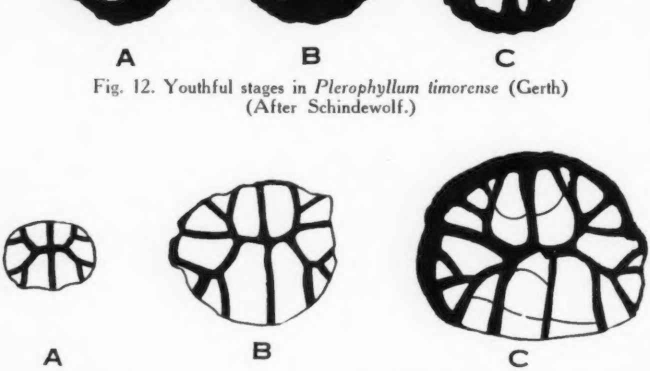
From this comparison of tetracorals and hexacorals, and from the characteristics of the intermediate genera, Weissermel concluded that the hexacorals are the direct descendants of the tetracorals, the propagation taking place through a very limited number of genera which by virtue of their favorable location were able to survive the rigorous conditions of the Permian.

Weissermel's views have since been strongly supported by Otto Schindewolf, who has carried further the studies on Permian forms. (1930, 1930a, 1931). From an analysis of the literature, and from his own studies on the tips of the Paleozoic corals, Schindewolf finds good evidence for attributing a primary bilaterality to the tetracorals. He contends that the bilateral disposition of the septa is primitive, and the later pseudo-radiality is the result of environmental conditioning, being especially the result of a sessile habit.



A B C

Fig. 12. Youthful stages in *Plerophyllum timorense* (Gerth) (After Schindewolf.)



A B C

Fig. 13. Early stages in the development of *Hapsiphyllum konincki*, (Edw. & H.) (After Schindewolf).

Richter's Study of the Operculates

The study of the operculated corals, which had already been carried to a high stage by Lindström, received a further important contribution through the researches published in 1929 by Rudolph Richter. Considering first the origin of the plano-convex form and the remarkably parallel growth lines of *Calceola, Richter* endeavored to show that these are but natural consequences of the possession of an articulated operculum. He contended that a broad, even edge is a mechanical necessity for the production of a satisfactory joint,

and once this is achieved, the flattened side and parallel strippings result merely from continued growth, and are not functional. There will thus be as many flattened sides as there are opercula, the number varying from one, in *Calceola,* to four, in *Goniophyllum.*

Richter agreed with Lindström in holding that whereas the calyx of the operculates is homologous with the calyx of other tetracorals, the operculum is an entirely new structure, and is not duplicated in the remainder of the *Rugosa.*

Conclusion

If, from the preceding summary, we endeavor to seek out those data which seem firmly established, and may thus be employed as tools for the future analysis of corals, we find that there is still relatively little which is beyond the pale of controversy.

Evidence is steadily accruing in favor of the initial hexameral character of the tetracorals, and concomitantly favoring the phylogenetic relationship of the tetracorals and the hexacorals. The factors inducing a suppression of the counter quadrants in the tetracorals, and thus producing a secondary tetrameral symmetry, are still uncertain, but seem assignable to mechanical changes arising from environmental adjustments. The ontogeny of corals is yet a relatively unexplored field, whose possibilities are only emphasized by the works of Duerden, Carruthers, and Salée.

In the study of the corallum itself we are on firmer ground, but here too there is a wealth of uncertainty. The secretion of the calcareous material of the skeleton has been given diverse interpretation by Lacaze-Duthiers, Ogilvie, and Bourne. The fossula has been described in turn as a gonidial groove, a mechanical consequence of sagging tissues, and an outlet canal for food bearing currents. Even such apparently simple apparati as the tabulae are susceptible to a broad range of explanations, as witness Bernard's concept of protothecae; and the function of such specialized appliances as the columella is almost wholly unknown.

On the other hand, the study of the septa has been carried to a high stage of perfection by Pratz, von Heider, and Ogilvie, and the nature of septal insertion has been clearly delineated. Von Koch has similarly done excellent work on the study of the theca, and his researches, together with those of Nicholson and Studer, have combined to give us a full understanding of asexual reproductive forms.

In the field of technique modern students have made marked strides, and the employment of grinding or slicing to produce serial sections, together with the improvements in the use of the camera and camera lucida as means of depiction, is the foundation of all our progress in the paleontology of corals.

It is in the classification of corals that we find the least advance has been made. This event, however, is to be expected, since progress in classification is dependent upon progress in all other branches of study. The systematizations of Milne-Edwards and Haime, or of Zittel, are still the authoritative

ones to-day. Perhaps the most marked suggestion of progress is W. D. Lang's proposal of "trends" as a means of grouping, but this is far from being a formal classification, and is at best but a re-vamping of the concept of type genera urged by Thomson and Nicholson. We are still far removed from a natural classification of the corals, based upon true kinship rather than upon chance resemblance of form, but the growing mass of data on ontogeny and homeomorphy seems to assure us of eventually achieving this end.

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NEW SPECIES OF FABULARIA, ASTEROCYCLINA, AND LEPIDOCYCLINA FROM THE FLORIDA EOCENE*

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I. Introduction

The junior author** in his work with samples from the wells drilled in Florida, either in connection with possible oil discovery or for water supply, encountered specimens of the genus *Fabularia*. This genus has been reported from France, Egypt and Australia, but this is the first record of it from North or South America. Associated with the specimens of *Fabularia* in one well are numerous small foraminifera and rather numerous specimens of the genera *Asterocyclina, Lepidocyclina* and a single specimen of *Discocyclina*. Upon detailed study, it appears that all these forms are new with the possible exception of the species of *Discocyclina*. Because of the interest in connection with the discovery of *Fabularia,* it seems desirable to describe and figure these forms.

The validity of the new species of *Fabularia* probably will not be challenged, as this species is decidedly different from those previously described. The erection of new names for the two species of orbitoids associated with *Fabularia* may be open to difference of opinion. *Asterocyclina monticellensis* sp. nov. is very near *A. chipolensis* Vaughan (1928) and *Lepidocyclina ariana* sp. nov. is closely related to a form described as *L. hubbardi aurarensis* by Mrs. Helen Hodson (1926).

While the writers were able to study a number of specimens and sections of *A. monticellensis,* the exact features which characterize *A. chipolensis* were not observed in these. As there are apparent differences and as these two species may be of importance in stratigraphic work the writers have applied a new name to their specimens.

As Vaughan has pointed out in several of his papers, the specific or varietal nomenclature of the larger foraminifera presents perplexing problems. A problem, similar to the one presented by *L. ocalana* and its allies which Vaughan (1928) so ably clarified recently, is presented by *L. trinitatis* H. Douvillé and its related forms. Mrs. Hodson (1926) has described a number of species and subspecies from Trinidad and Venezuela, some of which apparently are within the specific variation allowable for typical *L. trinitatis,* others should probably be recognized as varieties of *L. trinitatis,* while a few are such extreme variations that they should be classed as separate species. Rutten and Vermunt (1932) have attempted such a revision in part for the *L. trinitatis* group.

The present writers are particularly concerned with the form described by

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Mrs. Hodson as *L. hubbardi aurarensis*. The figures of this form indicate that it is closely related to the specimens to which we are applying the name *L. ariana*.

At the present time, the writers do not feel sufficiently well informed concerning the *L. trinitatis* group to suggest the relationships of the various forms one to the other. The figures given by Mrs. Hodson, however, indicate that *L. hubbardi aurarensis* is specifically different from the types which should be grouped under the name *L. trinitatis*. Rutten and Vermunt (1932) have retained this subspecies, but give very little information concerning its characteristics.

Unfortunately, not much detailed information is given by Mrs. Hodson (1926) concerning *L. hubbardi aurarensis* in the original description. Our ideas are based on a study of the two external views and the one vertical section of this form which were published. The writers have concluded that the form described by Mrs. Hodson is closely related to the one from Florida, but that these two forms can be separated one from the other in light of our present knowledge.

The writers wish to express their appreciation to Dr. T. Wayland Vaughan for reading this paper.

II. Description of Species

Genus *Fabularia* Defrance, 1820

Until the discovery of representatives in Florida, this genus has been reported only from the Eocene of France and Egypt and the Miocene of Australia. The characters of the genus make it easily recognizable. While the discovery in Florida greatly enlarges its geographic distribution, it will, likely, be reported from points in the West Indian and Caribbean regions as more detailed work is done upon the Eocene there.

Fabularia vaughani, sp. nov.

Plate 1, figs. 1-9

Description.—Test elongate oval, compressed parallel to the plane of coiling, the degree of compression variable, with blunt ends, ranging in length from 0.8 mm. to 2.6 mm. Most of the larger specimens are apparently microspheric individuals. Some of the smaller megalospheric individuals are more globular in shape. The holotype is 2.5 mm. long, 1.5 mm. wide and 1.0 mm. thick. The exterior of the test is composed of but two chambers. The suture can only be observed in well preserved specimens. The surface is ornamented by rather heavy costae which are discontinuous. The various portions of a costa are slightly offset one to the other, at the breaks. The aperture is poorly preserved in most specimens, but in the exceptional case where it is preserved the cribrate character is indicated.

The bilocular character of the outer chambers is clearly seen in transverse sections. The labyrinthic character of these chambers is apparently the result

of the incorporation of the costae into the chamber. In some cases there is secondary thickening. The canals thus formed are simple in all sections observed, except in a few cases, where there is a small secondary canal or opening developed. The section of *F. discolithes* introduced for comparison shows the canal complicated by a smaller secondary series in practically every instance in the outer chambers.

Figure 5, plate 1 represents a transverse section of a microspheric individual. The quinqueloculine character of the initial chambers has been almost entirely destroyed by replacement. The triloculine series is barely preserved. The biloculine character of the outer chambers is well shown; the jagged points represent the attachment of the second chambers which were destroyed in grinding. Figure 4, plate 1 is a longitudinal section of a microspheric individual showing the overlap of the biloculine chambers.

The megalospheric individual figured on plate 1, figure 6 has a spherical initial chamber 216μ in diameter. Figure 7 of the same plate represents a longitudinal section of a megalospheric individual whose initial chamber is subspherical in shape.

Holotypes and paratypes. — No. S-2426, Florida State Geological Museum.

Remarks. — *Fabularia vaughani* resembles slightly figures 8c and 8d given by Schwager (1883) for his *Fabularia zitteli.* The costae of *F. zitteli* are uninterrupted and heavier than those of *F. vaughani.*

Dr. Cushman kindly gave us specimens of *F. discolithes* Defrance from the Lutetian (middle Eocene) at Chaussy, France. A transverse section and external view of this form has been introduced on plate 1 for comparison with *F. vaughani.* These figures show the differences both internally and externally between *F. discolithes* and *F. vaughani.*

This species is named in honor of Dr. T. Wayland Vaughan, Director of the Scripps Institution of Oceanography at La Jolla, California.

Occurrence. — Ocala limestone (Eocene) from a well (F.S.G.S. no. W-72c) drilled by Gibbs Dry Dock Company, South Jacksonville, Duval County from a depth of 900 feet and from a well (F.S.G.S. no. W116) near Jacksonvile, Section 15, Township 2 South, Range 25 East owned by Mr. J. L. Quattlebaum from a depth of 860 to 900 feet. In these wells the zone in which this species occurs is from 360 to 400 feet below the top of the Ocala limestone.

In a well drilled by the Southern States Oil Company (F.S.G.S. no. W-19) about one and a half miles north of Monticello, Section 17, Township 2 North, Range 5 East,, Jefferson County, there occurs at 1740 feet specimens of *Fabularia* which appear to be identical to those found in the Jacksonville wells. These specimens are not as well preserved as those from the Jacksonville wells, but apparently exhibit the same characters. In this well the top of the Ocala limestone is at about 400 feet. Thus, this species must have a comparatively long vertical range. This might be expected as conditions were probably very stable during the deposition of the Eocene in Peninsula Florida.

In two thin sections from a limestone core taken between 4518 and 4531

feet from the Miami Oil and Gas Company's well (F.S.G.S. no. W-147) located about 40 miles west of Miami, in Section 19, Township 54 South, Range 35 East, Dade County, there are forms which may be safely referred to the genus *Fabularia*. One of these sections is illustrated on plate 1 by figure 12. Whether this is the same species as that described above can not be stated from the information at hand. The top of the Ocala in this general region is at about 1000 feet.

A few adult specimens were found at a depth of 310 feet in the well (F.S.G.S. no. W-166) of the Suwanee Petroleum Corporation in Section 9, Township 15 South, Range 13 East, a few miles east of Cedar Keys, Levy County. These specimens occur about 300 feet below the top of the Ocala limestone.

Genus *Discocyclina* Gümbel, 1868
Subgenus *Discocyclina* Gümbel, 1868
Discocyclina, sp. indet.

Remarks. — Unfortunately, only one specimen referable to this subgenus was discovered in the samples in our possession. This specimen represents a very small, fragile form 2.5 mm. in diameter. The surface ornamentation is pronounced, being composed of regular concentric circles of small, rather sharp papillae. The test thins regularly from the center to the periphery. In its external appearance this specimen resembles very closely a form described by Mrs. Helen Hodson from Venezuela as *D. mirandana.* Without more specimens for sections, positive identification can not be given at this time.

Occurrence. — Undifferentiated Eocene from the Southern States Oil Corporation well (F.S.G.S. no. W-19) drilled about one and one half miles north of Monticello, in Section 17, Township 2 North, Range 5 East, Jefferson County. The specimen came from a depth of 1740 feet.

Subgenus *Asterocyclina* Gümbel, 1868

Five species and a variety of this subgenus have to date been reported from the Ocala limestone of Florida. They are *A. americana* (Cushman), *A. chipolensis* Vaughan, *A. georgiana* (Cushman), *A. mariannensis* (Cushman), *A. mariannensis* var. *papillata* (Cushman) and *A. vaughani* (Cushman). Of these, only *A. chipolensis* is to date confined to Florida.

These forms are locally abundant and wherever found prove excellent stratigraphic markers.

Asterocyclina monticellensis, sp. nov.
Plate 2, figs. 6-11

Description. — Test small, radiate, robustly lenticular. The diameter between the bases of the radii varies from 1.2 to 1.7 mm.; thickness from 0.6 mm. to 0.8 mm. The rays, 6 to 8 in number, can not be observed over the central area of the test, but near the margins they become pronounced, projecting in some cases as much as 0.7 mm. beyond the margin of the test. The surface of the radii is raised and smooth. The interradiate and central por-

tion of the test is strongly papillate, the papillae increasing in size toward the central area. Usually there is a small boss over the center.

The embryonic apparatus consists of a spherical to subspherical initial chamber partially embraced by a larger chamber. In three specimens the initial chamber is spherical, about 90μ in diameter, in another specimen the chamber is subspherical with a length of 180μ and a width of 127μ. The distance across both chambers varies from 180 to 215μ. Outside the embryonic apparatus proper, and before the rectangular equatorial chambers commence, there is a partial circle of chambers which are variable in shape.

The equatorial chambers are rectangular, the length commonly 2.5 times the width. The average length of the chambers in the outer annuli is 75μ. The radial chamber walls of adjacent annuli usually alternate in position, but some of them are in alignment. As seen in the vertical sections, the equatorial layer is very thin and of nearly the same thickness from the center to the periphery. The height is about 35μ, including the walls of the floor and roof.

The lateral chambers are arranged in regular tiers, the number of chambers to a tier over the center varying from 10 to 12. The height of the chambers of the outer layers including both walls is about 30μ; the length about 70μ. Heavy pillars are present; those over the center have a diameter near the periphery of the test of 100 to 125μ.

Cotypes. — No.S-2424, Florida State Geological Museum.

Remarks. — As noted in the introduction, *A. monticellensis* is very close to *A. chipolensis* Vaughan. It is smaller than *A. chipolensis,* has fewer lateral chambers to a tier and has a decidedly different surface ornamentation. The surface of *A. chipolensis* is pitted, while that of *A. monticellensis* is strongly papillate.

Later, it may be found preferable to consider *A. monticellensis* a variant of *A. chipolensis.* At the present time, however, the authors feel that no difficulty will be found in readily separating these two species.

Occurrence. — Undifferentiated Eocene from the Southern States Oil Corporation's well (F.S.G.S. no. W-19) drilled about one and a half miles north of Monticello, in Section 17, Township 2 North, Range 5 East, Jefferson County. The depth at which this species occurs is 1740 feet, which depth is 1340 feet below the top of the Ocala limestone, uppermost Eocene.

Genus *Lepidocyclina* Gümbel, 1868
Subgenus *Lepidocyclina* Gümbel, 1868

Lepidocyclina (Lepidocyclina) ariana sp. nov.

Plate 2, figs. 1-5

Description. — Test small, discoidal, the diameter of megalospheric individuals average about 2.4 mm.; the thickness averages about 0.60 mm.; microspheric individuals were not observed. The surface of the test is covered with rather strong papillae, the papillae are especially pronounced over the central area of the test.

There are two subequal, rather large embryonic chambers which are di-

vided by a straight wall. The length of the two chambers is about 450μ; width about 360μ; thickness of wall about 35μ.

The equatorial chambers are of two intergrading types. Most of the chambers have curved outer and converging inner walls; some of the chambers near the periphery are diamond shaped. The chambers near the periphery have a transverse diameter of about 110μ and a radial diameter of about 90μ. The height near the center of the test, including both the floor and roof, is about 125μ. There is apparently little increase or decrease in height as the periphery is approached.

There are only two or three layers of lateral chambers to a tier over the center. The chambers are irregularly arranged in most cases although some are arranged in rather regular tiers. The length of the chambers is variable ranging from 50 to 90μ; the height is rather constant, about 30μ. The walls are thick, often nearly as thick as the chamber cavity. Pillars are present.

Cotypes. — No. S-2425, Florida State Geological Museum.

Remarks. — The equatorial section of *L. ariana* resembles that of *L. trinitatis* H. Douvillé. Other closely related forms are *L. pustulosa* H. Douvillé and *L. sherwoodensis* Vaughan. Mrs. Hodson described a form under the name *L. hubbardi aurarensis* which is very closely related to our species.

The Florida specimens have heavier papillae which are more uniformly distributed over the surface of the test, the cavities of the lateral chambers are pronounced, and these chambers are more regular in their development compared with the figure of *L. hubbardi aurarensis*. The ratio of thickness to diameter is different than that indicated by Mrs. Hodson's illustrations for her species.

Occurrence. — Undifferentiated Eocene from the Southern States Oil Corporation's well (F.S.G.S. no. W-19) drilled about one and a half miles north of Monticello, Section 17, Township 2 North, Range 5 East, Jefferson County, from a depth of 1740 feet, or 1340 feet below the top of the Ocala limestone, uppermost Eocene.

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THE OHIO STATE UNIVERSITY, AND
TALLAHASSEE, FLORIDA.

PLATE I

Figs 1-9. *Fabularia vaughani* sp. nov.

Fig. 1. External view of a paratype; x 14.

Fig. 2. External view of the holotype; x 14.

Fig. 3. Natural section through a paratype showing internal arrangement; x 30.

Fig. 4. Longitudinal section through a microspheric individual; paratype; x 30.

Figs. 5–6. Transverse sections of paratypes; figure 5, a microspheric individual; figure 6, a megalospheric individual; x 30.

Fig. 7. Longitudinal section through a megalospheric individual; paratype; x 30.

Figs. 8–9. Transverse sections through two probable microspheric individuals showing variation of internal arrangement; the specimens resembled figure 1; paratypes; x 30.

Figs. 10–11. *Fabularia discolithes* Defrance.

Fig. 10. Slightly oblique transverse section introduced for comparison; x 30.

Fig. 11. External view introduced for comparison; x 14.

Fig. 12. *Fabularia* sp.; x 30.

(Specimens represented by figures 1, 8 and 9 from a depth of 900 feet from well (W-72c); those represented by figures 3 to 7 are from a depth of 860-900 feet from well (W-116); while those represented by figures 10 and 11 are from Chaussy, France. Figure 12 represents a portion of thin section from a limestone core from the Miami Oil and Gas Company well, (W-147) about 40 miles west of Miami at a depth of 4518 to 4531 feet.)

PLATE I

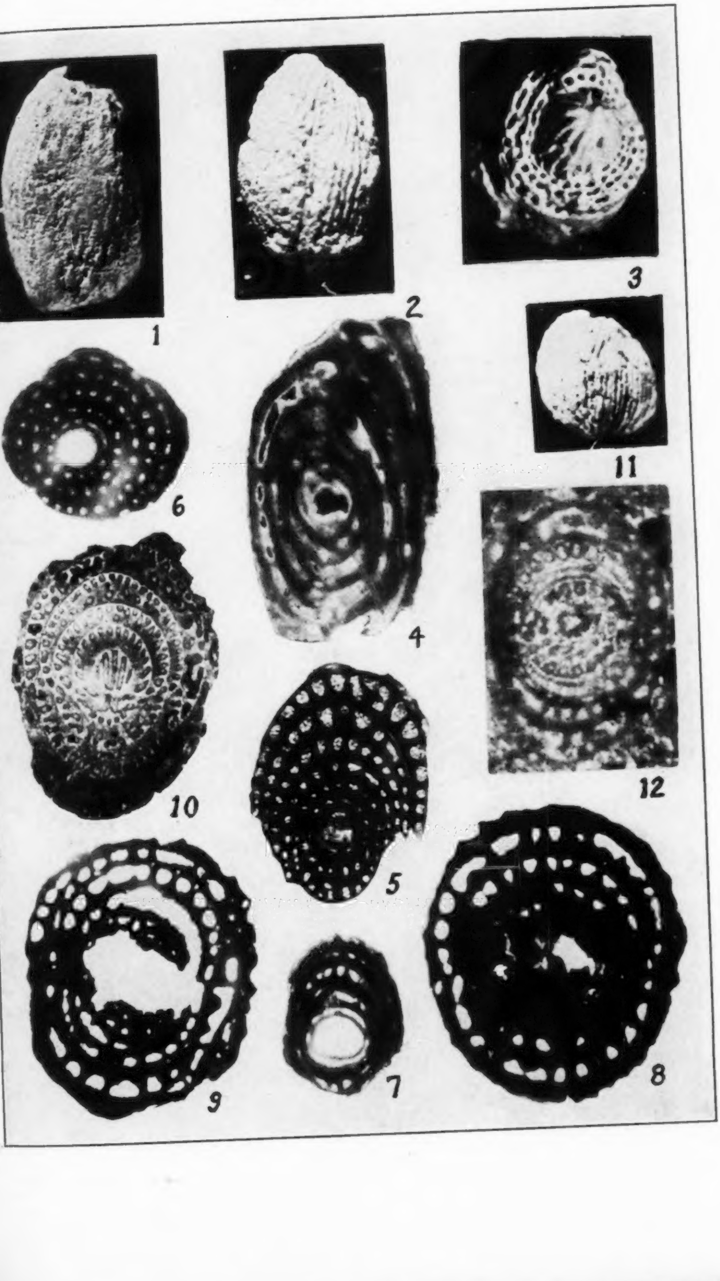


PLATE II

Figs. 1-5. *Lepidocyclina ariana* sp. nov.

Fig. 1. External view showing the papillate character of the surface; x 14.

Fig. 2-3. Vertical sections of two cotypes; x 30.
Figs. 4-5. Horizontal sections of two cotypes; x 30.

Figs. 6-11. *Asterocyclina monticellensis* sp. nov.

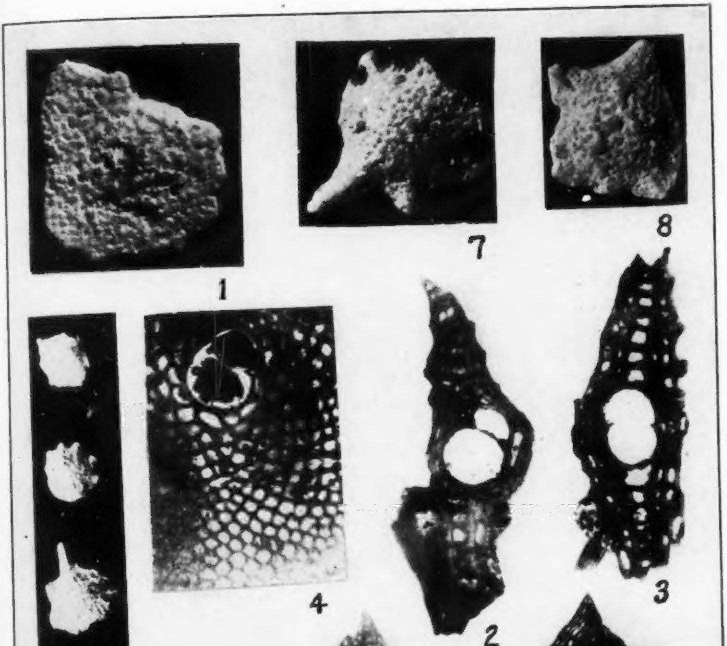
Figs. 6-8. External views to show general radiate outline and surface ornamentation; figure 6, x 6; figures 7 and 8, the two bottom specimens of figure 6, x 14.

Fig. 9-10. Vertical sections; x 30.

Figs. 11. Horizontal section, showing the embryonic apparatus, equatorial chambers and portion of one ray; x 30.

(The specimens figured on this plate are all from a depth of 1740 feet from the Southern States Oil Corporation well, drilled about one and a half miles north of Monticello, Jefferson County, Florida.)

PLATE II



NEW ARTIODACTYLS FROM THE OLIGOCENE AND LOWER MIOCENE OF NEBRASKA

HAROLD J. COOK

I. Introduction

During the past twenty-five years, the writer has accumulated fossil Artiodactyla from the many Oligocene and Lower Miocene exposures of northwestern Nebraska. Many of these were given field records, but until recently were neither catalogued nor studied. Yet they contain both new occurrences and new taxonomic groups, which extend the reported range of certain races both downward into the Lower Oligocene, and upward through distinct formations into the Lower Miocene beds. In addition, certain new forms of the Middle Oligocene are recognized, along with many specimens of known species, which are not discussed in this paper.

While some of these types are less complete than we could wish, it seems important to describe them at this time, in order to extend our available records of these rare forms, of which types are preserved in the Cook Museum of Natural History, Agate, Nebraska. All specimens described in this paper were found by the writer unless otherwise noted.

II. Summary

The evidence at hand indicates that, while certain branches of the Oligocene *Leptomeryx* group are probably ancestral to *Blastomeryx* in the Lower Miocene, as determined by Matthew, other branches of this group may be ancestral to other cervids of Upper Miocene and Lower Pliocene beds, but hardly can be ancestral to *Blastomeryx;* and that at least one branch, that represented by *L. agatensis,* described herein, persisted into Lower Miocene times, probably as a contemporary of *Blastomeryx,* comparatively little changed from its Oligocene ancestry.

The little Upper Oligocene species of *Hypisodus* described herein has premolar characters which are more suggestive of the pecora than the Stenomylid camels; and represents an intermediate and distinct branch of diminutive size, extending the known range of this race upward to the end of White River times. The Lower Oligocene species, *H. paululus,* described herein, is the smallest species so far discovered and extends the known range of the race downward to the beginning of the White River deposits.

The relative of *Protoceras* described herein ("False-Protoceras," as the name implies) is an interesting race, and it is to be hoped that more complete remains will be found of this peculiar creature, which is the oldest known Oligocene near-relative of the Upper White River *Protoceras.*

III. Description of Species

Order ARTIODACTYLA Owen

Suborder PECORA Linnaeus

Family *Protoceratidae* Marsh

Pseudoprotoceras longinaris gen. nov. et sp. nov.

Plate 3, fig. 1.

Generic Characters. — Upper dentition: $I.^0$; $C.^1$; $P.^4$; $M.^3$. Marked recession of anterior nares; premolars simple, and molars more progressive and hypsodont than in *Protoceras* and *Heteromeryx;* skull relatively flat, with facial portion elongated.

Description. — The skull, so far as preserved in the genotype, is remarkably flat, and more like that of *Protoceras* than any comparable genus. Even though allowance is made for the fact that the type has had the frontals and nasals compressed downward, it still remains a very flat skull. No distortion of the palate, maxillae or premaxillae has taken place, so that most characters can be determined so far as they are preserved in the type.

The frontals between the orbits, and the posterior end of the nasals, are very rugose. Two osseous enlargements of peculiar form are located where the small pair of "median horns" occur just in front of the orbits in *Protoceras.* No suggestion of maxillary horns like those of *Protoceras* is seen; but the upper ridges of the elongated maxillae are ditched and roughened as for strong muscular attachments. The whole region of the superior surface of the skull, from the back of the orbits forward, suggests well developed muscular attachments and a muzzle more tapiroid than cervid-like in its development, but of a distinct type. The facial region is even more elongated, in relation to its size, than in *Protoceras;* and the maxillae and premaxillae extend forward to a marked degree.

The posterior nares extend forward in the palate as far as the posterior borders of the first molars, expand most widely at the rear of the second molar, and contract again toward the pterygoids. No palatine foramina are present. The premaxillae extend 17 mm. in front of the alveolar border of the canines.

The alveoli and maxillae indicate long, slender laniary canines, much as in *Blastomeryx.* The incisors are absent. P^1 was very small, and situated about 4 mm. behind the canines. Back of this is a diastema 10 mm. long. P^2 is a simple trenchant tooth, much as in *Hypertragulus,* and more primitive than in *Protoceras, Leptomeryx, Heteromeryx* or *Trigenicus.* P^3 is like P^2, but with a low deuterocone connected by a cingulum extending each way to the anterior and posterior ends of the tooth; and differs from the corresponding tooth in the above named genera. P^4 like that in the above genera, but with the median external ridge prominent as a rounded swell, distinctive from the conditions seen in these forms.

The upper molars have parastyle, mesostyle, metastyle, and both external ribs strongly developed. A pillar is developed from the cingulum on the antero-internal faces of both crescents of each molar. This is a large, strong

pillar on the inside of the last crescent of M^3, strongly suggestive in a primitive condition of the developments seen in later races of cervids and bovids. The posterior is largest on each molar. These developments from the cingulum are most prominent on M^3, and progressively smaller in M^2 and M^1. A suggestion of similar cusps in an incipient state is seen in some specimens of *Leptomeryx* and other genera.

While brachydont, the dentition is more nearly hypsodont than is the case in the more recent *Protoceras* of the Upper Oligocene. This and other characters mark it as already having progressed too far in certain directions to be ancestral to *Protoceras;* seemingly representing a nearly related branch, or race. Its teeth are less brachydont than *Heteromeryx,* and more comparable in that character to the condition noted in *"Leptomeryx" mammifer* Cope.

The associated astragalus and navicular were found pressed against the palate. The tibular end of the astragalus has a distinctly cervid aspect. The other end is more suggestive in its "cut" and slight lateral twist of the condition seen in certain entelodonts and peccaries, and is unlike that of cervids, bovids or oreodonts. There is more of an inward twist between these two ends than in the Oligocene or later camels. The tarsal elements are not fused, and there is a sharp, elevated keel between the navicular and cuboid facets.

Dimensions

Length of skull, tip of premaxillae to back of last molar	96 mm.
Width of palate at P^2	15 mm.
Width of palate at M^2	22 mm.
Length, P^2 to M^3, inclusive	53 mm.
Length, M^1 to M^3, inclusive	30 mm.

	P^1.	P^2.	P^3.	P^4.	M^1.	M^2.	M^3.
Length,	3	8	9	6	9	10	11
Width,	1.5	3	6	8	10	12	11

Remarks. — This race has undoubted affinities with *Protoceras,* which genus, so far as reported, is restricted to the Upper Oligocene (Protoceras Beds); but it contains characters which seem to preclude it as a direct ancestor to that genus, though undoubtedly near the ancestral line.

This species is much smaller than *Protoceras;* smaller than the contemporary *Heteromeryx dispar* Matthew; larger than *Trigenicus socialis* Douglas; and approaches the size of *"Leptomeryx" mammifer* Cope.

The recession of the anterior nares is remarkable, extending slightly back of the anterior rim of the orbits, though the nasal bones are relatively longer than in *Protoceras celer* Marsh. This character agrees most closely with *Protoceras,* and differs radically from *Heteromeryx, Trigenicus, Leptomeryx, Hypertragulus, Hypisodus,* and other genera.

Part of the lower jaw, No. HC508, of an old individual, with three well worn teeth preserved, and found in the same horizon and locality, a short distance away, is provisionally referred to this species; other fragmentary specimens in the collections may also belong to it.

Holotype. — No. HC507, Cook Mus. Nat. Hist. — The anterior portion of a skull, virtually complete from the orbits forward; one astragalus and navicular.

Occurrence. — Lower Chadron (Lower Oligocene) beds about 9 miles north of Crawford, Nebraska, in the same horizon and locality as the type of *Hypertragulus chadronensis*, and several other races.

Family *Hypertragulidae*

Hypertragulus chadronensis sp. nov.

Plate 4, fig. 1

Description. — This species is most readily distinguished from *H. calcaratus* Cope by its smaller size, more slender and somewhat more brachydont dentition. The posterior crescents of M_3 are united posteriorly into a crescent. In size, it was between *H. calcaratus* (found in the Middle Oligocene Oreodon beds) and *H. minutus* Lull, from the Upper Oligocene John Day beds; but nearer the former. Cingulum is absent on M_1, and but slightly developed, and interrupted, on M_2 and M_3, being less well developed than in any *H. calcaratus* specimens I have examined; though this character is not shown in some published figures.

Dimensions

	H. calcaratus Type	*H. chadronensis*
Length, M_1 to M_3, inclusive	17.5 mm.	16 mm.
Length, M_3	8 mm.	7 mm.
Width, M_3	7 mm.	4.5 mm.

Remarks. — Great similarity exists in many characters in these Hypertragulids, but it is probable that when more complete materials are discovered, many distinguishing characteristics will be found in these forms from distinctly different horizons, not available in the present specimens.

Holotype. — No. HC501, Cook Mus. Nat. Hist. — Part of a well preserved right lower jaw, with M_1-M_3, inclusive. This is the first reported species from the Lower Oligocene (Chadron formation). It was found by the writer about nine miles north of Crawford, Nebraska, in the lower part of the Chadron formation, only a few feet above the contact with the marine Pierre shales.

Hypertragulus crawfordensis sp. nov.

Plate 4, fig. 12

Description. — Characterized by its large size, this species is slightly larger and more hypsodont than the contemporary *"Leptomeryx" mammifer* Cope; and distinctly more hypsodont than the contemporary *Heteromeryx*. The "heel" on the last lower molar has the external and internal crescents united, in the manner characteristic of *Hypertragulus*, and not separated by a fissure posteriorly, as in *Leptomeryx*. Aside from the difference in size, the patterns of these teeth is strikingly similar to those noted in the diminutive species described herewith, from the same horizon, *H. chadronensis*.

Dimensions

Length, M_1 to M_3, inclusive	31 mm.
Length, M_3	13 mm.
Width, M_3	8 mm.

Remarks. — The writer also has in these collections representatives of this large race of Hypertragulus, of closely comparable size, from both the Lower and Upper Brule, indicating that it persisted throughout White River time; but in view of the fragmentary condition of these specimens, no further description will be given at this time.

Holotype. — No. HC550, Cook Mus. Nat. Hist., part of right lower jaw, with the three true molars fully developed, and moderately worn down.

Occurrence. — Lower Chadron formation, north of Crawford, Nebraska.

Hypertragulus quadratus sp. nov.

Plate 4, fig. 7

Description. — This species is based upon a portion of a skull, with the three upper left molars from an individual with fully developed, but almost unworn teeth. It compares most closely, among described species, to *H. minutus* Lull of the Upper John Day beds of Oregon, and is distinctly smaller than the typical *H. calcaratus* Cope, of the Lower Brule.

A tiny, cusp-like process on the external cingulum is suggestive of an incipient development of the mesostyle, while a comparable development is found on the corresponding internal side of each molar, between the crescents. All molars are distinguished from those of *Nanotragulus* by their tendency to be quadrate, rather than elongate postero-anteriorly.

Dimensions

Length of upper molars	14 mm.
Length, M^3	5 mm.
Width, M^3	5 mm.

Remarks. — Its size and the marked difference in geologic age are the most obvious differences on which this species is now distinguished; but again, more complete material undoubtedly will bring other distinguishing characters to light. Other specimens of this race in our collections, from the same beds, merely emphasize the characters cited, but are too fragmentary to add much information, as the premolar region and other important parts are missing. The type, however, bridges part of the gap which has existed in described forms between *Hypertragulus* and *Nanotragulus,* and while a distinct gap is yet present, it tends to emphasize the close relationship between them.

Holotype. — No. HC590, Cook Mus. Nat. Hist. — Left maxilla with M^1-M^3.

Occurrence. — Upper Brule, about eight miles northeast of Harrison, Nebraska.

Hypertragulus sequens sp. nov.

Plate 3, fig. 2

Description. — This species probably will prove to belong to a distinct genus when more complete material is found. The teeth are strikingly more hypsodont than in any previously described Hypertragulid, and contain strongly developed columns in all of the external valleys, even the posterior valley of M_3. This character, as well as the whole cut of the teeth, is strongly suggestive of cervid relationships, but is too advanced to suggest this as a probable ancestor of any known Lower Miocene race. This species rather suggests types met in the Upper Miocene and Lower Pliocene.

Dimensions

Length, M_1 to M_3, inclusive	20	mm.
Length, M_3	9	mm.
Width, M_3	3.5	mm.
Length, M_2	6	mm.
Length, M_1	5	mm.

Remarks. — Fossils are rare in these beds and this is the first evidence of Hypertragulids to be found in them, so far as I am aware. *H. ordinatus* Matthew, from the Lower Rosebud beds, to the eastward, of equivalent age, has less hypsodont and less specialized teeth.

Holotype. — No. HC502, Cook. Mus. Nat. Hist. — Part of a right lower jaw, with M_1 to M_3, inclusive.

Occurrence. — This specimen was found in the Upper Oligocene Monroe Creek beds, near Monroe Creek, north of Harrison, Nebraska, about 100 feet above the top of the Brule.

Leptomeryx antecedens sp. nov.

Plate 4, fig. 8

Description. — Distinguished by extreme obliquity of the lower molars; smaller than the typical *L. evansi* Leidy. The teeth also appear to be more brachydont, but owing to their state of wear that character is not certain. The molar series expand at M_2 and taper rapidly forward to P_4. Likewise the anterior part of M_3 is wider than the central crescents, and the third, or posterior crescents, are much smaller, contrasting in this respect markedly with other described species of the genus.

Dimensions

Length, M_1 to M_3, inclusive	20	mm.
Length, M_1	6	mm.
Width, M_3	4.5	mm.
Length, M_1	6	mm.
Width, M_1	4	mm.

Remarks. — Among described species, this Lower Oligocene form most closely approaches the Upper Oligocene *L. obliquidens* Lull, from the Protoceras beds, and may well be ancestral to this larger species. While apparently closely related to the *L. evansi* race, it probably represents a parallel group that had separated from the others by the opening of Oligocene times.

Fragmentary specimens noted by the writer from Middle Oligocene (Brule) beds, add evidence to make this probability more certain.

Holotype. — No. HC504, Cook Mus. Nat. Hist. — A left lower jaw, with P_4 to M_3, inclusive.

Occurrence. — Chadron formation, about twenty miles northwest of Harrison, Sioux County, Nebraska.

Leptomeryx exilis sp. nov.

Plate 3, fig. 3

Description. — This species is distinctly smaller than the fairly abundant *L. evansi* found in the same beds. The most distinctive character, aside from smaller size, is the diminutive posterior internal crest. The posterior external crest is strongly developed. A paratype, mentioned below, represents an animal about the size of the above holotype, and consists of a part of the facial portion of a skull. This shows some interesting characters. Most conspicuous of these, the orbits extend over P^4 and nearly to P^3, much farther forward than in *L. evansi.* The frontals and nasals slope down at a sharp angle, forward, to where they are broken off, and indicate a much shorter face than in that form. In P^3 the deuterocone stands out as a distinct pillar, not connected as in other described species. As these characters cannot be determined in the type of *L. exilis,* no direct comparison is possible at this time, and this may not represent a distinct species.

Dimensions

Length, M_1 and M_2	13	mm.
Width, M_1	3.5	mm.
Length, M_1	7	mm.

Remarks. — The holotype was found by the writer in the Brule (Middle Oligocene) beds about two miles north of Chadron, Nebraska, in 1907. Since that time the writer has found other specimens of this form in the Oreodon (Brule) beds, but all rather badly broken up and fragmentary. Another specimen, (No. HC506) Cook Mus. Nat. Hist., collected at nearly this same horizon, but in northern Sioux County, Nebraska, by Miss Hilda Wilson, is described above.

Holotype. — No. HC182, Cook Mus. Nat. Hist. — Part of a right lower jaw, with the posterior two molars.

Occurrence. — Brule (Middle Oligocene) beds, about two miles north of Chadron, Nebraska.

Leptomeryx lenis sp. nov.

Plate 4, figs. 2-3

Description. — This species is slender and somewhat smaller than *L. evansi* of the Middle Oligocene, and the teeth are more hypsodont. The premolars are reduced in size, and the facial region was evidently distinctly shorter, as indicated by the shortened anterior end of the mandible. The diastema between P_1 and P_2 is distinctly shorter and barely 2 mm. long. P_2 was evidently very slender; P_1 much as in *L. evansi.* The incisiform canine and the incisors were evidently very small, slender, and procumbent.

P_3 and P_4 are distinctly approaching the pattern found in *Blastomeryx olcotti*, of the Lower Miocene, as compared with that of *L. evansi*. They are narrow, and the three internal crests are not separated by as deep valleys as in *B. olcotti*. This intermediate condition suggests a form somewhere near the ancestral line through which the latter was derived.

The upper molars are more hypsodont than in *L. evansi*, but differ little otherwise. P^4 is slightly reduced in size relatively, and has a distinct cingulum on the postero-internal side of the deuterocone, but not developed as far as in *L. agatensis*, to which it is closely related, and to which it may be ancestral.

Dimensions

Length, P^4 to M^3, inclusive	23 mm.
Length, M^1 to M^3, inclusive	19 mm.
Length, M^2	6 mm.
Width, M^2	8 mm.
Length, lower jaw, M_3 to tip of symphysis	54 mm.
Length, P_2 to M_3, inclusive	40 mm.
Length, M_1	6 mm.
Length, M_2	7 mm.
Length, M_3	10 mm.
Width, M_2	4.5 mm.

Holotype. — No. HC503, Cook Mus. Nat. Hist. — Parts of both maxillae, with P^4 to M^3, inclusive; the right lower jaw with P_3 to M_3, inclusive, and alveoli and roots of the anterior teeth, including incisors.

Occurrence. — Found in a small exposure near the top of the Upper Brule, at the foot of the Miocene escarpment on Sowbelly Creek, northern Sioux County, Nebraska. The skull and jaws were weathering out, and a recent hard rain had washed away missing parts, but the parts preserved were so associated in position in the matrix, as to indicate clearly that they belonged to one individual.

Leptomeryx agatensis sp. nov.

Plate 4, fig. 6

Description. — *Leptomeryx agatensis* appears to be most closely related, among the described species, to *L. transmontanus* Douglas, the details of the teeth being closely similar. The deuterocone of P^2 is connected to the posterior edge of the tooth by a thin ridge, as in that type, and in this type differs from *L. evansi*. No cingulum is found on P^3, and an incipient cingulum is present on the internal side of P^4, best developed on the postero-internal face of the deuterocone.

Dimensions

Length, P^3 to M^3, inclusive	29 mm.	Length, M^3	6 mm.
Length, M^1 to M^3, inclusive	19 mm.	Width, P^3	5 mm.
Length, P^3	6 mm.	Width, P^4	6 mm.
Length, P^4	4 mm.	Width, M^1	7 mm.
Length, M^1	6 mm.	Width, M^2	8 mm.
Length, M^2	7 mm.	Width, M^3	7 mm.

Remarks. — *Leptomeryx agatensis* is smaller than *L. transmontanus*, and the premolars are relatively smaller and compressed, suggesting a skull with a shorter face. The teeth are set more obliquely in the maxilla; the mesostyle is somewhat less strongly developed on the molars, and the anterior external rib is relatively better developed. From this type, it appears that the *Leptomeryx evansi* race of Middle Oligocene times has persisted, little changed in dentition, into the Lower Miocene, in this same region.

Holotype. — No. HC500, Cook Mus. Nat. Hist. — A left maxilla with P^3 to M^3, inclusive, from a mature individual.

Occurrence. — This specimen was found in Syndyoceras Hill, one-half mile west of Agate, Nebraska, in the fossil-bearing horizon which seems to be identical with the "bone level" in the Agate Springs Fossil Quarries, located about four miles to the eastward, in the Lower Harrison formation, (Lower Miocene).

Hypisodus paululus sp. nov.

Plate 4, fig. 9

Description. — About one-sixth smaller than *H. alacer* Troxell of the Middle Oligocene Brule, this tiny species is further characterized by very simple, narrow teeth, more slender than in the other known species. Metastyle more prominent on all lower molars than in *H. alacer;* last crescent on M_3 not so well developed as in the latter form, but all teeth surprisingly hypsodont for such an early species.

Dimensions

Length of three lower molars	10 mm.
Length of third lower molar	4 mm.
Width of third lower molar	1.3 mm.
Depth of jaw below M_2	5 mm.

Remarks. — This species is of special interest as it is both the oldest and the smallest known member of this, the tiniest known race of Artiodactyla; and is undoubtedly the ancestor of *H. alacer* Troxell, its nearest known relative. As an interesting comparison, a small fossil rabbit jaw, *Protolagus* cf. *affinis* Walker, found quite near it in the same bed, dwarfs it by comparison. It is hard to see how such a race could have survived in the presence of the many and far larger carnivora which were its contemporaries throughout its known range, now embracing the whole of White River Oligocene time.

Holotype. — No. HC552, Cook Mus. Nat. Hist. — A left lower jaw with the true molars preserved, mature, and little worn.

Occurrence. — Lower Chadron formation, about nine miles north of Crawford, Dawes County, Nebraska.

Hypisodus ironsi sp. nov.

Plate 4, fig. 10

Description. — Compared with *H. alacer*, the hypsodont molars are even more slender, and P_4 is more cervid-like and more reduced in size than the broken P_4 in the type of *H. alacer* would indicate. A diastema 3 mm. long is present in front of P_2, extending to where the jaw is broken off, and was evidently longer. P_2 is less than half a mm. wide, and less than 1 mm.

long. P_3 is two-rooted, but simple; 2 mm. long and very thin. P_4 is reduced in size, more like *Leptomeryx* in type, but is simplified, and is more suggestive of a cervid than it is of *Stenomylus*, to which its molars bear such striking similarity in type, though, of course, the two are of vastly different size.

The molars are very slender, and the slight tendency to develop ribs on the outside of the molars is more comparable to the condition seen in the Miocene *Blastomeryx* than it is to the condition found in *Stenomylus*.

Dimensions

Length of three lower molars	11 mm.
Length, M_3	5 mm.
Width, M_3	2 mm.
Length, P_2 to M_3, inclusive	18½ mm.
Length, P_3 to M_3, inclusive	17 mm.

Remarks. — The present form is smaller than the genotype of *Hypisodus*, (*H. minimus* Cope) smallest of known Artiodactyl genera. It also is smaller and more slender than the tiny *H. alacer* Troxell, of the Middle Oligocene Oreodon beds. The occurrence of this new species at the top of the Brule extends upward the known vertical range of the family.

The beautiful little jaw on which this species is founded was discovered by Mr. Charles R. Irons, of Scottsbluff, Nebraska, for whom it is named and through whose kindness the writer has been permitted to study and describe it.

Holotype. — No. 505, Cook Mus. Nat. Hist. — A right lower jaw, P_2 to M_3, inclusive; loaned by Charles R. Irons.

Occurrence. — Top of the Brule (Upper Oligocene) beds at the base of the Gering formation exposures at the south end of Scotts Bluff, near Mitchell Pass, just west of Gering, Nebraska.

Family *Cervidae* Goldfuss

Blastomeryx pristinus sp. nov.

Plate 3, fig. 4

Description. — Molars larger and more hypsodont than those of other known Lower Miocene species of *Blastomeryx*. External ribs and styles on the upper molars present, as in *Leptomeryx* and *Blastomeryx*, but less strongly developed, save along the postero-external ridge, which is relatively more strongly developed than in the known species of these genera, and more comparable to the condition in various Cervidae and Bovidae of Upper Miocene and Pliocene times. The metastyle is reduced almost to the vanishing point. The internal pillar is relatively less developed than in *Leptomeryx*, and much less than in the known species of *Blastomeryx*. The condition of the internal crescents is intermediate between that noted in the Middle Brule species of *Leptomeryx*, and the Upper Harrison species of *Blastomeryx*.

Dimensions

Length, M^2	14 mm.
Width, M^2	12 mm.
Height of crown of partly worn tooth, above base of enamel	9 mm.

Remarks. — The present evidence establishes the presence of a rather large cervid with more hypsodont and simple molars than those known previously from these Lower Miocene beds, but with characters indicating descent from some race of *Leptomeryx;* yet clearly not ancestral to the known races of *Blastomeryx* found in the overlying and later formations. It may prove to be ancestral to certain little-known cervids of the late Miocene and Pliocene, and may be quite distinct from *Blastomeryx,* to which it is referred, when more complete evidence is found. As it occurs in the same geologic horizon as the type of *Leptomeryx agatensis,* it furnishes definite evidence of the fact that descendants of that Oligocene genus were diverging and the genus splitting up into diverging races in Miocene times. This is the oldest species referred to date to the genus *Blastomeryx,* the oldest previously known having been found in the overlying Upper Harrison beds.

Holotype. — No. HC669, Cook Mus. Nat. Hist. — A left upper molar. Other isolated teeth from the same level in these collections, confirm these characters, but add no new information of importance.

Occurrence. — Lower Harrison beds. Found in the Agate Springs Fossil Quarries, Agate, Nebraska.

Blastomeryx cursor sp. nov.

Plate 4, figs. 4-5

Description. — P_2 is large and has a deuterocone connected by a cingulum to the posterior end of the tooth. It is nearly connected in the same way anteriorly, but is separated by a valley internally. P_3 is like P_2, but is larger and heavier, with the deuterocone completely connected by a heavy cingulum anteriorly. The anterior lobe of these premolars is relatively heavier than in *Leptomeryx,* and slightly more complex. A close comparison shows these characters to be entirely explicable as minor developments from the earlier *L. evansi* pattern. P_4 is closely like that of *Leptomeryx.* These premolars are more primitive than those of any of the other known species from the Lower Miocene, and all cheek teeth are but little more hypsodont than those of the Oligocene races of *Leptomeryx,* in relation to size.

The quadrate molars are all strikingly alike, with parastyle and mesostyle, the anterior external ridge heavy, and the posterior ridge incipient. All have a small internal pillar. The internal end of the posterior crescent of the molars is long and extends well up between the external crescents, farther than in the other Lower Miocene races of *Blastomeryx,* more as in the Middle Miocene *(Blastomeryx) Dyseomeryx riparius,* and in modern *Mazama.* The posterior end of the anterior crescent is short, as in other closely related species, but between this and the internal end of the front crescent of each molar there is a crenulated enamel pillar on all molars, connected to both internal crescents, that makes a conspicuous complexity of enamel pattern distinct from the teeth of described Lower Miocene species.

The lower molars are most readily distinguished from contemporary species of *Blastomeryx* by their greater size, though minor differences are noted. Internal pillars are well developed in the lower molars, and a short cingulum appears on the front of the antero-internal crescents.

Dimensions

Length, P^2 to M^3, inclusive	59 mm.
Length, M^1 to M^3, inclusive	32 mm.
Length, P^1	9 mm.
Length, P^2	10 mm.
Length, P^3	8 mm.
Width, M^2	12 mm.
Width, M_2	7 mm.
Length, metatarsals	148 mm.
Width, distal end of metatarsals	22 mm.

Remarks. — This is the largest species of Lower Miocene *Blastomeryx* so far reported, having primitive premolars, little altered from those of Leptomeryx, with advanced molar pattern. The evidence furnished by it greatly strengthens the evidence that *Blastomeryx* is a descendant of Leptomeryx, although there evidently were diverging lines of descent.

Holotype. — No. HC142, Cook Mus. Nat. Hist. — Part maxillae and upper teeth from both sides, P^2 to M^3; two lower molars and parts of limbs and feet.

Occurrence. — Upper Harrison (Lower Miocene) beds, found in 1907 about four miles northeast of Agate, Nebraska.

Blastomeryx tantillus sp. nov.

Plate 3, figs. 5-6

Description. — About half the size of *B. cursor,* with molars of closely similar type, but more simple. Internal pillars absent or vestigial, on both the upper and lower molars; cingulum nearly absent. The enamel complications between the two internal crests of the upper molars are simpler and less well developed than in *B. cursor.* The postero-external crest of M_3 is primitive and even less well developed than in any Oligocene species of *Leptomeryx* known to the writer. It is much more primitive than that in other described species of *Blastomeryx,* in that character more nearly approaching the condition seen in *Machaeromeryx tragulus.* Metapodials are fused, and like those of *B. advena, B. cursor,* and related species, but smaller.

Dimensions

Depth of jaw below M_2	8 mm.
Length, M_2	7 mm.
Length, M_3	10 mm.
Length, M^2	7 mm.
Width, M^2	7 mm.
Width M_2	4.5 mm.
Width, distal end of metacarpals	11 mm.

Remarks. — This is not only the smallest species of *Blastomeryx* so far discovered after more more than thirty years of collecting in these beds, but it is the smallest of the known true Pecora, being even smaller than the contemporary *Machaeromeryx tragulus,* and nearly the size of *Leptomeryx.* This species is not derivable, morphologically, from any Oligocene race of

Leptomeryx known to the writer, unless processes of evolution are reversible, and may well go back to an earlier point of division. However, an undescribed race occurs in the Upper Snake Creek beds, in about a Middle Pliocene stage, bearing characters more progressive but clearly derivable from the present race, and distinct from other species at present assigned to the genus *Blastomeryx*.

Holotype. — No. HC241, Cook Mus. Nat. Hist. — Part of a left lower jaw with M_2M_3; two upper molars; and parts of a foot, associated.

Occurrence. — Upper Harrison beds, three miles northeast of Agate, Nebraska.

Nanotragulus matthewi sp. nov.

Plate 4, fig. 11

Description. — The molars are simple, but far more hypsodont than those of *Hypertragulus;* likewise the crowns above the base of the enamel, in worn teeth, judging by the least worn molars in these specimens, are at least twice as tall as in *L. agatensis*. The molars are relatively long and narrow, antero-posteriorly, and the species is larger than that form. Both external ribs are prominent on all molars; parastyle slight on M^1; fairly prominent on M^2 and M^3; mesostyle absent as in *Hypertragulus;* metastyle incipient on M^1, slight on M^2, and but moderately developed on M^3. Molars simple and without cingulum.

Dimensions

Length, M^1 to M^3, inclusive	21 mm.
Length, M^1	6 mm.
Length, M^2	7 mm.
Length, M^3	8 mm.
Greatest height of enamel on M^2 (base to top, partly worn down)	7 mm.

Remarks. — The teeth of *Nanotragulus matthewi* are distinctly more hypsodont than in *H. ordinatus* Matthew, from the Lower Rosebud beds of South Dakota.

As compared with *Nanotragulus loomisi* Lull, it is about twenty per cent larger, the molars are more hypsodont and the crowns are long, anteroposteriorly, and narrow, being somewhat more quadrate in that type. The parastyle is less developed, especially in M^1.

As noted by Lull and Matthew, this genus shows distinct relationships to *Hypertragulus*, and the present species is the most advanced in type of this group, in point of hypsodonty, paralleling the development, to a lesser degree, of the condition seen in the earliest known type of *Merycodus*, described herewith.

This species is named in honor of the late Dr. W. D. Matthew, in recognition of his valuable researches in this group, and in appreciation of many years of invaluable contact and associations, both in the field and laboratory.

Holotype. — No. HC332, Cook Mus. Nat. Hist. — Part of a left maxilla with three molars, well preserved.

Occurrence. — Found in the Lower Harrison beds, Lower Miocene,

in the same level as the type of *Leptomeryx agatensis* described herewith, and within forty feet of the spot where the type of *Syndyoceras cooki* Barbour was found by the writer, all in the same horizon, and but a short distance apart.

Family *Antilocapridae* Grey
Merycodus prodromus sp. nov.

Plate 3, fig. 7

Description. — Smaller than any described species of *Merycodus*, with somewhat less hypsodont molars than those of the known, and geologically later, species of the genus. Molars simple, narrow and hypsodont, without cingulum or internal pillars; anterior rib on upper molars prominent; posterior one nearly absent, in this character agreeing closely with *Leptomeryx* on the one hand and *Merycodus* on the other. Molars long and narrow as in later species of *Merycodus*, rather than quadrate, as in *Blastomeryx* and *Leptomeryx*. Compared with *M. necatus* they are smaller, less hypsodont, and the mesostyle is less prominent; the parastyle smaller.

Dimensions

Length, M^2	9 mm.
Width, M^2	7 mm.
Height of crown above base of enamel (partly worn down)	8 mm.

Remarks. — This is the earliest known occurrence of the genus *Merycodus*, and the smallest species with the least hypsodont molars, which narrows the gap previously existing between this genus and *Leptomeryx*. Examination of a series of Upper Miocene and Lower Pliocene specimens of the genus, belonging to *M. necatus* and closely related species, shows a consistency of type present in molar characters, but considerable variation in the degree to which the postero-external enamel rib on the molars is developed, it being, in some specimens rather distinct; in a few, practically absent.

The proportions of the molars of *M. prodromus*, while larger, are also very similar to those of *Nanotragulus matthewi*. *M. prodromus* differs from that form in the presence of a strong mesostyle. In *N. matthewi* both external enamel ribs are about equally developed, and swelled outward, in a manner suggestive of *Blastomeryx*, though the teeth are more hypsodont. These characters indicate parallel development, but also suggest diverging lines of descent from *Leptomeryx* in the one case, and from *Hypertragulus* in the other, as elsewhere suggested in this paper. This species is probably directly ancestral to the Upper Miocene *M. necatus*, so far as can be judged from known characters, which differ merely in degree, being more primitive.

The skull had been tramped upon by stock and almost totally destroyed and the teeth were collected under adverse circumstances; but there is no doubt that they belonged to the same individual.

Holotype. — No. HC512, Cook Mus. Nat. Hist. — Two second upper molars, from a single individual, from a badly disintegrated skull.

Occurrence. — Upper Harrison beds, four miles north of Agate, Nebraska.

AGATE, NEBRASKA.

PLATE III

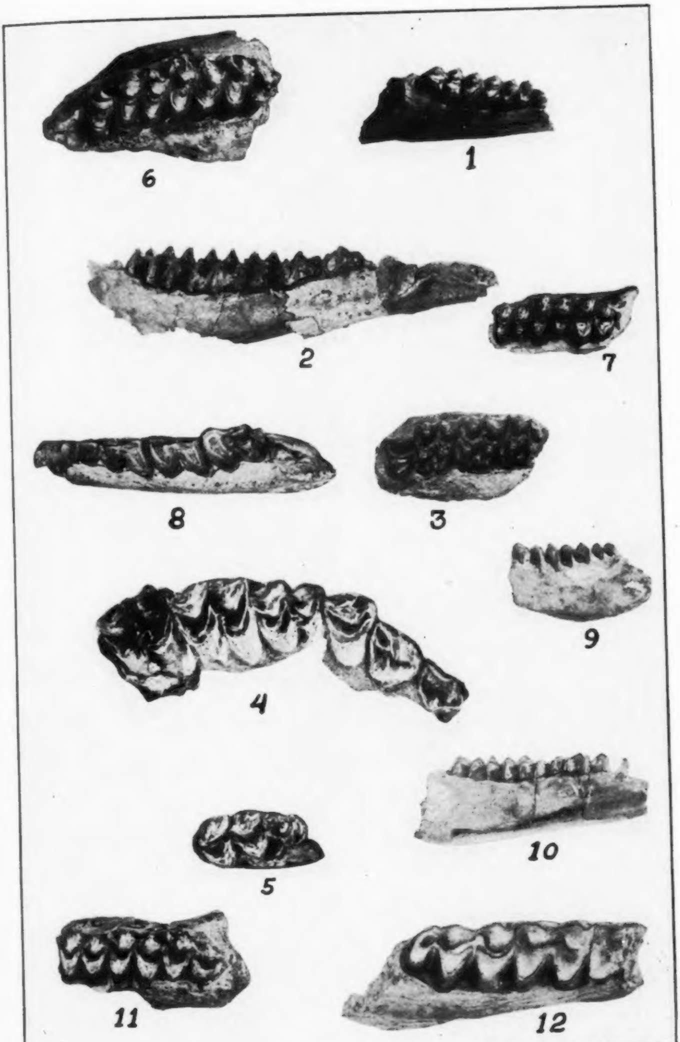
Fig. 1. *Pseudoprotoceras longinaris*, n. sp. Holotype, x 1.
Fig. 2. *Hypertragulus sequens*, n. sp. Holotype, part of right lower jaw, x 1
Fig. 3. *Leptomeryx exilis*, n. sp. Holotype, part of right lower jaw, x 1.
Fig. 4. *Blastomeryx pristinus*, n. sp. Holotype, upper M^2, left, x 1.
Fig. 5-6. *Blastomeryx tantillus*, n. sp. Holotype.
Fig. 5. One upper molar, x 1.
Fig. 6. Part of left lower jaw, x 1.
Fig. 7. *Merycodus prodromus*, n. sp. Holotype, two upper molars, x 1.

PLATE III

PLATE IV

Fig. 1. *Hypertragulus chadronensis*, n. sp. Holotype, part of right lower jaw, x 1.10.
Fig. 2-3. *Leptomeryx lenis*, n. sp. Holotype.
Fig. 2. Right lower jaw, x 1.10.
Fig. 3. Part of left maxilla with molars and last premolar, x 1.10.
Fig. 4-5. *Blastomeryx cursor*, n. sp. Holotype.
Fig. 4. Upper right molars and last three premolars, x 1.10.
Fig. 5. Lower last molar, x 1.10.
Fig. 6. *Leptomeryx agatensis*, n. sp. Holotype, left maxilla with molars and last two premolars, x 1.25.
Fig. 7. *Hypertragulus quadratus*, n. sp. Holotype, left upper maxilla (part) with molars, x 1.25.
Fig. 8. *Leptomeryx antecedens*, n. sp. Holotype, part of left lower jaw, x 1.25.
Fig. 9. *Hypisodus paululus*, n. sp. Holotype, part of left lower jaw, x 1.25.
Fig. 10. *Hypisodus ironsi*, n. sp. Holotype, right lower jaw, x 1.25.
Fig. 11. *Nanotragulus matthewi*, n. sp. Holotype, part of left maxilla, with three molars, x 1.25.
Fig. 12. *Hypertragulus crawfordensis*, n. sp. Holotype, part of right lower jaw, x 1.25.

PLATE IV



THE NATURAL HISTORY OF CALLIANASSA CALIFORNIENSIS DANA

G. E. MacGINITIE

The mud-dwelling shrimp *Callianassa californiensis* Dana (1854) is one of the most abundant animals to be found in the muddy ground of marine sloughs or bays on the west coast of North America. Its reported range has been from Mutiny Bay, Alaska (Lockington) to the mouth of the Tia Juana River, San Diego County California (Rathbun (1921). The present writer has taken it as far south as El Estuario de Punta Banda, Lower California.

Callianassa is considerably elongated, which is possibly a direct response to its method of living, and is rather brightly colored, even though always hidden in the mud. Adult individuals average from two to three inches in length and vary from a whitish yellow to orange-red. Their one outstanding feature is the possession of an exceedingly large cheliped (see Pl. 5), which may be either the right or left. This inequality in size of the chelipeds is largely a dimorphic trait, for in the females it is not nearly so marked. Specimens used for study in the preparation of this paper came mainly from Elkhorn Slough, a salt water estuary situated at the east side of Monterey Bay, California. The laboratory work was done at the Hopkins Marine Station of Stanford University and at the Kerckhoff Marine Laboratory, and field work was carried on along the entire coast of California.

The habits of this shrimp may be observed readily for it may be kept indefinitely in limoria at the laboratory. The limoria used were frames holding two plates of glass (nine by sixteen inches) about three-quarters of an inch apart, filled three-quarters full of mud and submerged in aquaria. Artificial burrows were also made of glass tubing. These were quite satisfactory, although not so good as limoria, for reasons that will be seen later. The shrimps must be kept in glass tubes, or where they can burrow; because they soon die if kept where the sides of their body are not in contact with some object.

Function of Appendages.—When *Callianassa* is walking, it uses the third, fourth, and fifth pairs of legs. The fourth pair of legs are extended laterally and held in an elevated position so that they subserve the very important function of balancing and supporting the animal by bracing it firmly against the walls of its burrow. The legs of the fifth pair are so bent that the propodi and dactyls are beneath the abdomen, thus giving a pigeon-toed effect.

This animal swims by the use of its swimmerets, with the large cheliped held directly ahead. It attempts swimming only upon necessity, and then only for short distances. It also can move quickly backward, which is a general characteristic of all shrimps, by means of several flips of the tail fan.

The legs have other functions equally as important as that of locomotion. The large cheliped is used as a weapon of offense and defense. It can pro-

tect the carapace (see Pl. 5, fig. 3), and since these shrimps are continually encountering one another it serves to do battle for disputed ground and during mating season, a fact that may account for the larger cheliped on the males. Other crustacea with which we are familiar, for example, *Upogebia* (1930), *Crangon, Betaeus,* and *Pachycheles,* that live in more or less permanent burrows in pairs, do not show noticeable dimorphic characters.

The second and third pairs of legs are used as shovels in digging. The fourth feet are employed for cleaning the mouth parts, the bases of the antennae, and the anterior portions of the carapace. The short, stiff setae of the propodus and dactyl make an efficient brush for this purpose.

The fifth feet are used to clean the back, the inner surface of the branchiostegite, and the gills. They are also used for scrubbing the pleopods, and ovigerous females frequently spend several minutes manipulating the eggs with the delicate chelae of these legs.

While the animal is resting or performing cleaning operations the swimmerets move more or less constantly, which serves to keep water circulating through the burrow for respiratory purposes. The tail fan can block the burrow quite effectively, and therefore may be used as a protective device to ward off attacks from the rear.

Callianassa comes in contact with its environment almost exclusively through the hair-like structures which are present in greater or lesser numbers over the surface of its body. This may be more true of *Callianassa* than of most other shrimps, even mud-dwellers, for the eyes are degenerate, each having less than 100 facets.

Microscopic examination of these hairs, together with close observation of the habits of the shrimps, revealed that the hairs are of vital importance. They function mainly in the following ways:

1. For obtaining food
   - a. Sifting sand
   - b. Scraping and moving sifted food to the mouth
2. For cleaning
3. For creating currents
4. For carrying eggs
5. For receiving stimuli

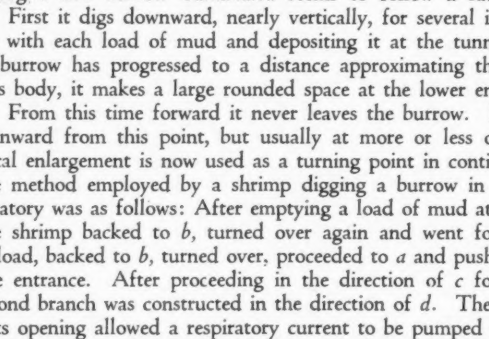
There are many distinct types of hairs, and modifications of these occur in different regions of the body, so that in the final analysis the mapping of these structures become quite complicated. Most of the hairs have primary and secondary feathering. Important types are shown in Plate 6.

Burrowing.—Callianassa is found most abundantly in tidal regions of from zero to plus one foot, and is restricted to bottoms of mixed sand and mud of a sufficiently tenacious consistency to allow the construction of burrows of a rather permanent nature. Neither very loose sand nor very soft mud will serve.

The animal is occupied almost constantly in extending or adding new tunnels to its burrows, which often connect with those of other individuals.

Such connections, however, are continually being blocked off and tunneled around. The chelae of the first and second legs serve for digging and drawing the sand backward, then the palps of the third maxillipeds rake it backward and upward into the receptacle formed by the ischium-merus of the third maxillipeds (Pl. 5, figs. 2 and 4). The third legs often assist in this process by a forward pushing movement. After a load of mud is gathered it is carried to the opening of the burrow and pushed outside mainly by the second chelae.

In digging a new burrow *Callianassa* seems to follow a rather definite procedure. First it digs downward, nearly vertically, for several inches, backing outside with each load of mud and depositing it at the tunnel entrance. When the burrow has progressed to a distance approximating the length of the shrimp's body, it makes a large rounded space at the lower end to enable it to turn. From this time forward it never leaves the burrow. It continues to dig downward from this point, but usually at more or less of an angle. The spherical enlargement is now used as a turning point in continued operations. The method employed by a shrimp digging a burrow in a limorium at the laboratory was as follows: After emptying a load of mud at *a* (see text figure), the shrimp backed to *b*, turned over again and went forward to *c*, obtained a load, backed to *b*, turned over, proceeded to *a* and pushed the load through the entrance. After proceeding in the direction of *c* for some distance, a second branch was constructed in the direction of *d*. The completion of *d* with its opening allowed a respiratory current to be pumped through the burrow. Other tunnels may be extended in any direction until the burrow becomes very much branched and complicated, and at the points where one tunnel joins another there is usually an enlarged space or "turn around." There are from two to several openings to a burrow. There seems to be no stimulus which controls or directs the activity of the shrimps. They, apparently, "just burrow."



These animals seem to be moving almost constantly. What time they are not busied in working over the sand and carrying it away, they spend in cleaning their appendages, gills, and back. Such careful and constant sanitary measures are probably necessitated by the nature of their habitations. In fact, in spite of all their diligence, microscopic examination reveals minute fungus growths on the setae of these creatures.

As mentioned above, *Callianassa* burrows are abundant where conditions permit, and they perforate the sand in every direction. The number of these animals and their constant activity leads one to conclude that they subserve much the same function for the bottom soil of estuaries that the earthworm does for the field. Their tunnels sometimes extend downward as far as any

of the other forms of life exist; and because of these tunnels other species of animals living in the mud are supplied with fresh water, and the deeper sand is constantly being brought to the top.

Feeding.—*Callianassa* feeds by sifting the sand for its contained detritus. As in burrowing, the sand is drawn in from the face of the tunnel; but, unlike the actual burrowing, the sand is sifted by the hairs on the dactyls of the second and third legs and is scraped off by the hairs of the third maxillipeds. From these by a series of movements of the mouth parts, it finds its way to the oesophagus. The method of sifting is the opposite of that usually employed by screens, for the coarse material is allowed to drop through, while the fine material is picked up by the hairs of the legs and maxillipeds and ingested. These hairs are very efficient for the purpose, and are shown in detail in Plate II. Undigestible material exceeds the digestible, the sorting of the material ingested taking place in the stomach. After sifting, the load is picked up, carried to an entrance, and deposited outside.

The stomachs of these shrimps are suited admirably for dealing with abrasive substances, such as sand; and they do not have, as does the crayfish, a large cardiac portion for the storage of food. With such a diet, the problem of storage does not enter; but rather that of working over a large amount of sand to extract a sufficient quantity of food. It is for this reason that burrows of glass-tubing are not so good as limoria; for, while *Upogebia* (1930), which feeds on suspended material, gets along nicely in a glass burrow, *Callianassa* will in time starve.

A sifted load of sand for an average-sized *Callianassa* will approximate one-half to one cubic centimeter. The amount of material deposited around one entrance between low tides (that is, a twenty-four hour period ranges from twenty to fifty cubic centimeters, which is equivalent to a layer one-eighth inch thick over the entire area occupied. At this rate the soil would be turned over in 240 days to a depth of thirty inches, which is the approximate limit of depth to which the animals burrow. These figures are conservative. The surface of the bottom of sloughs continually has deposited upon it a grey scum of detritus, which upon being covered by the excavated material is continually worked deeper. For this reason the upper regions are more fertile in food material and the burrowing activities are carried on mainly within the upper eighteen to twenty inches. As a consequence, this region must be entirely turned over every few months. The following conditions confirm this idea. An area of about one-half acre, where *Callianassa* was as abundant as at any place in the Slough, was covered and built up by drifting sand to an extent that it was left uncovered for longer periods by tides, with a resulting diminished deposit of detritus. The *Callianassa* disappeared from this area within a few months, though the length of time the area was covered with water would have been sufficient under normal conditions for food getting. No sand is brought to the surface except when the entrances of the burrows are submerged. The author thinks that the number of individuals of *Callianassa* living in the mud is near the maximum that the deposit of detritus will support, and that starvation will be general if this is over-reached. The

loss of large numbers will decrease the amount of detritus buried by excavation deposits; conseqeuntly, the sterile or cleaned conditions of the subsurface soil will make it impossible for even a few individuals to sift a sufficient quantity of sand between tides to obtain food in an amount necessary to sustain life.

Conditions continually are being made suitable for the establishment of colonies of *Callianassa*. Where the tide exposes the bottom, conditions are changing constantly and there is a continual succession. These changes are brought about mainly by the following factors: (1) tidal currents, (2) plant growth, (3) animal activities, and (4) winds. These factors exert their influence in the following way. A region is built up by tidal currents until it is sufficiently close to the surface at low tide to support a growth of *Enteromorpha* and other surface algae. This growth then aids the deposition of sand, which often covers it. The mud afterward turns black by the action of purple bacteria. Within two or three months this ground is in excellent condition for mud dwellers, especially *Callianassa*, owing to the abundance of organic matter. This organic matter also makes the mud firmer and helps to retain the material subsequently deposited. The activities of the animals prevent, to a great extent, further cover growths of *Enteromorpha*, so that, as the region continues to build up, it is exposed for greater lengths of time between tides. Finally the mud is sifted clean of organic material and when drying wind lightens the upper surface, some blows away, the remainder washing away with incoming tidal currents. Thus, the whole surface is again lowered, algal growth is renewed, and another succession takes place, the drifting sand from a worn-out region helping to start a new one. Within my experience of six years at Elkhorn Slough and Newport Bay, by adding together observations from several areas, I have seen the completion of such a cycle. It is by no means my intention to convey the idea that the above procedure is uniform. The increase of the effectiveness of a factor in this or that region, or the addition of others, destroys any semblance of regularity, and ten years would, perhaps, be a short time for such a cycle. The length of time is somewhat regulated by the distance inland from the entrance of the slough or estuary. Near the entrance changes take place quite rapidly, relatively speaking, while in the more remote regions but little change may make itself manifest over long periods of time. Judging from the results of feeding experiments on *Urechis* and from stomach examinations of *Callaianassa*, I believe bacteria play a very important part in the food of this animal.

Additional Notes.—Ovigerous females may be found at any time throughout the year, but are more numerous during the latter part of June and July. The eggs are carried by the female until the embryos have reached the zoea stage, when hatching takes place. They subsequently pass through a cypris stage, and at the next molt become like the adult, and settle to the bottom. It is at this stage that the greatest mortality must occur. As has been stated in two previous papers (1930, 1928), the greatest mortality, at least at Elkhorn Slough, for mud-dwelling forms, is the few minutes, or possibly in some cases an hour or two, between the free-swimming condition and the stage

where establishment in the mud takes place. At this time they are at the mercy of all the surface feeders, which include many crustacea, worms, and even molluscs. Especially active in combing the surface of the bottom of the Slough for food is the tiny goby fish, *Clevelandia ios*. This small goby is a little over an inch in length, and a conservative estimate would place its abundance at an average of about one per square foot. With a few dips of a net I have screened over five hundred from a small pool about three by eight feet, where they had congregated when the tide was out. When *Clevelandia* is kept in an aquarium, it is seen to make little quick moves of an inch or two here and there over the bottom, occasionally picking up food particles unseen to the human eye. These fish undoubtedly find most mud-burrowing larvae before the latter are able to conceal themselves.

Juvenile specimens of any Slough species are rare, and *Callianassa* is no exception. After digging several thousand adults, I find that specimens under three-quarters of an inch average less than one in a hundred. An attempt is being made to determine growth rate in this animal; but, until this is done, one can not say definitely how much the above evidence points to longevity. However, this scarcity of young, together with the facts that there is no year grouping of individuals, that they have practically no enemies once they are established in the mud, and that a dead one is rarely seen, rather definitely shows that *Callianassa* lives several years at least.

Commensals.—There are seven macroscopic commensals which live with *Callianassa,* at least five of which may be present in a single burrow. Two are specific, *Hemicyclops callianassae* Wilson, a new copepod, and *Harmothoë* sp. nov., a polynoid worm. Two pinnotherids, *Scleroplax granulata* Rathbun and *Pinnixa franciscana* Rathbun, and a small clam, *Cryptomya californica* (Conrad), are commensal with *Upogebia* (1930) and *Urechis* (1928) as well as with *Callianassa. Clevelandia ios* (Jordan and Gilbert) is a small goby fish which makes use of the burrows of *Callianassa, Upogebia* (1930) and *Urechis* (1928) as a refuge, or while the tide is out. The seventh commensal is a new species of *Betaeus,* a small shrimp which lives in pairs in the burrows of *Callianassa.*

Since these commensals, together with their host, form a very interesting relationship which almost could be called a community, they are dealt with in turn at some length.

Hemicyclops is present in considerable numbers among the eggs of ovigerous *Callianassa.* It may feed to some extent on the eggs, but I believe mainly on the debris which collects, such as dead embryos, empty cases, and growths which the female shrimp fails to remove in her cleaning activities.

Juvenile *Harmothoë* live epizoically, lying across the abdomen between the swimmerets of ovigerous females, while the adults live freely in the burrow. *Harmothoë* are especially vicious towards each other; and two allied species, one commensal with *Urechis* and one with *Upogebia,* allow no intruders of the same or other species. But one therefore occurs in each burrow. As the burrows of *Callianassa* interconnect, and those of *Upogebia* and *Urechis* do

not, it may be that this habit of the juvenile *Harmothoë* living on *Callianassa* is a self-preserving characteristic and allows for the establishment of the young worms in the burrows. The *Harmothoë* are not so numerous in proportion to the adult *Callianassa* as are the polynoids which live with *Upogebia* and *Urechis*. The commensal subsists on the edible material uncovered by the burrowing and feeding activities of the shrimp. As was seen under the heading *Food*, *Callianassa* ingests no large particles, hence the discarded material consists, in part, of food material for the commensals, such as parts of dead animals or even live ones, and is admirably suited to the needs of the *Harmothoë* and the crabs. Food suitable for use by the commensals is also often brought in by aerating currents. *Harmothoë* has a short proboscis, 5 mm. in length, which it can evert with lightning-like rapidity. When two *Harmothoë* are fighting in a glass burrow in an aquarium, the eversion of a proboscis can be heard distinctly as a sharp snap through the glass of the tube, the water, and the glass of the aquarium. They attack any worms or other living forms that are used by them for food in the same manner; and, no doubt, as will be seen below, their food getting activities also help to furnish food for the commensal crabs. The fact that the polynoids commensal with *Urechis*, *Upogebia*, and *Callianassa* are distinct species, can perhaps be accounted for by the habits of the host with which they live. The polynoid commensal with *Urechis* lives in a burrow with but two entrances, and, also, it usually lies with its dorsal side close against the body of its host. The one dwelling with *Upogebia* lives in a rather extensive burrow; however, it, too, lives in a permanent burrow and with permanent hosts, i. e., with a pair of *Upogebia*. Those commensal with *Callianassa* do not even keep the same hosts, and are more or less in communication with each other.

Scleroplax granulata and *Pinnixa franciscana*, two Pinnotherids, live freely in the burrows, and also with *Upogebia* and *Urechis*. Both crabs have, on rare occasions, been found together in *Urechis* burrows, but never so far with *Callianassa*. The *Pinnixa* seems to be the larger and more aggressive crab, although both are good fighters, their authority being second only to that of the host. They are more plentiful than the *Harmothoë*, and they subsist, as does the latter, on the left-overs from the feeding, burrowing, and aerating activities of their host. When the polynoid secures a morsel that is too large for immediate swallowing, it is quickly lost to the crab, which scents its presence in the burrow. After the crab has eaten its fill, the remainder is discarded and the polynoid may return to what is left. Both of these crabs supplement their more solid diet by screening plankton—which consists mainly of bacteria and decaying plant material in suspension. This will be taken up in detail in a subsequent paper.

Although *Cryptomya californica* has short siphons, it may be found at a depth of 18 or 20 inches. This fact aroused the curiosity of the writer to the extent that subsequent investigations revealed that the clam lies close to the burrows of *Callianassa*, *Upogebia*, and *Urechis*, with its siphons projecting just within these burrows. This allows feeding currents to be maintained from the waters of the burrows. One at once wonders about the relative fares

in different burrows, for both *Urechis* and *Upogebia* strain their food from the currents they pump through the burrow, and *Urechis,* at least, has a more efficient food straining apparatus than the clam. However, food straining takes but perhaps one-fourth to one-half the time of either *Upogebia* or *Urechis* and, of course, is never carried on during low tide exposures. The clam, then, may feed during the other half or three-quarters of the time, and even when the tide is out the burrow contains water which may be rather rich in bacteria and protozoa. *Cryptomya,* being such a small clam, needs but little food, or perhaps is small because it gets but little. There are more *Cryptomya* in *Callianassa* beds, relatively speaking, than in other regions; but, on the other hand, burrows are also more numerous.

Clevelandia ios, a small goby fish, is a very interesting creature. It not only seeks shelter within the burrows of the above-mentioned hosts, but, as observed in the laboratory, it makes inspection trips throughout the length of the burrows, being perfectly at home at any depth and wriggling past its host whenever it wishes, to the entire indifference of the latter. If a large piece of, for example, clam meat, too large for a goby to swallow, is put into a burrow which also contains crabs the goby, after attempting to swallow or tear it apart, will carry the meat to a crab and stand by while the latter makes it smaller, the fish at intervals snatching it for another attempt at swallowing, to the disconcertion of the crab. This fish will do the same thing in an open aquarium with *Spirontocaris* present.

Betaeus sp. nov. inhabits the burrows of *Callianassa californiensis* in the southern limits of its range. Seven pairs were taken from the burrows of *Callianassa* during one evening's collecting at El Estuario de Punta Banda, Lower California. The fact that in all cases these commensals were found in pairs indicates that they live in this manner.

After an understanding of the life habits of an animal such as *Callianassa* is acquired, one appreciates the necessity for making intimate studies of the natural history of at least the more important members of an association.

Physical factors have been omitted from this paper, as they will be included in a future general paper dealing with Elkhorn Slough and its fauna.

Summary

1. *Callianassa californiensis* is abundant in mud flats of bays and estuaries on the west coast of North America.

2. Individuals are quite awkward and helpless outside their burrows.

3. The burrows are extensive and are being added to continually because the animals sift sandy mud for its contained detritus.

4. The food of *Callianassa* consists entirely of detritus.

5. The continual turning over of the soil and the aeration of the subsoil

by the burrows of this animal is important to the entire community of mud-dwellers.

6. Colonies of the shrimps show more or less regular succession.

7. These shrimps have seven commensals, ranging from *Hemicyclops callianassae* and *Harmothoë* sp. nov., which are specific, through the two crabs *Pinnixa franciscana* and *Scleroplax granulata*, the shrimp, *Betaeus* sp. nov., and the clam, *Cryptomya californica*, which may inhabit the burrows of other species also, to the goby, *Clevelandia ios*, which makes use of the burrow as a refuge or while the tide is out.

8. Knowledge of the intimate life histories of the more important members is essential to an understanding of an association.

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PLATE V

Fig. 1. Photograph of dorsal view of female, cheliped in usual position. x ¾.

Fig. 2. Photograph of lateral view of female. x ¾.

Fig. 3. Photograph of dorsal view of male, showing the chela in protective position. x 1.4.

Fig. 4. Photograph of ventral view of male. x 1.4.

PLATE V

PLATE VI

All figures in this plate are x 600, except 4b and 5b, which are x 145. The structures attached to the main portion of the hair are referred to as primary feathering, and the structures attached to the primary feathering are referred to as secondary feathering.

Fig. 1. For sifting sand. From the merus of the second leg. (Pl. 5, fig. 4). Those from the inner margin and inner face of the third maxilliped are similar, but are much shorter and lack the secondary feathering. Actual length of entire hair, 5 to 7 mm.

Fig. 2 and 3. For sifting sand. These hairs from the second maxilliped are about equally numerous and are intermingled along the inner margin of the endopodite. Actual length of hairs, 4 mm.

Figs. 4 and 5. For moving food to the mouth.

4a. From the inner margin of the basis of the second maxilla. Those of the first maxilla and first maxilliped are similar.

4b. A group of 4a.

5a. From the palp of the mandible.

5b. A group of 5a.

Fig. 6. For cleaning. This represents an entire hair from the brush of the fifth leg.

Fig. 7. For creating currents. From the outer margin of a swimmeret. Length of hair, 1.5 to 3 mm.

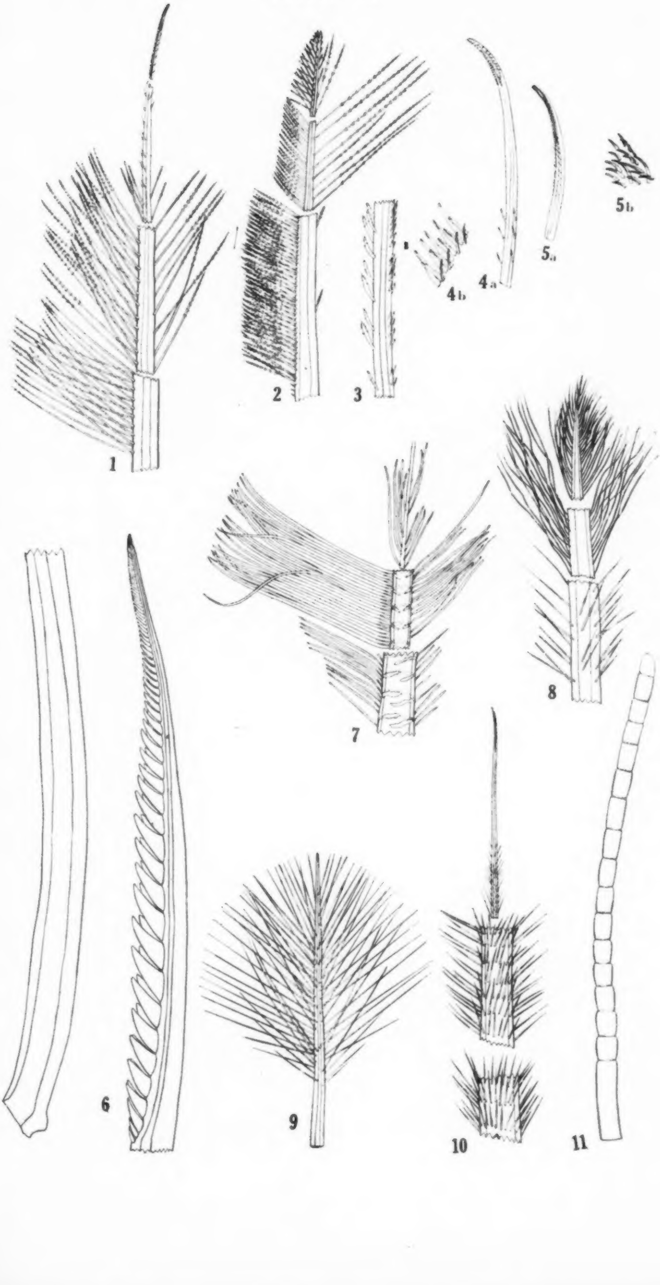
Fig. 8. For carrying eggs. From the endopodite of the first and second abdominal appendages. Length, 7 to 8 mm.

Fig. 9. For receiving stimuli. From the flagellum of an antenna.

Fig. 10. For receiving stimuli. From the outer margin of the outer ramus of the uropod.

Fig. 11. For receiving chemical stimuli. From the tip of the outer flagellum of an antennule.

PLATE VI



THE VARIATION AND DISTRIBUTION, RECENT AND FOSSIL, OF THE SNAIL POLYGYRA PROFUNDA SAY, IN ILLINOIS

FRANK C. BAKER

Polygyra profunda is a land snail that occurs abundantly in the northern portion of the United States and is one of the species most commonly encountered in the northern section of Illinois. It is known from early Pleistocene, during which period it seems to have been abundant. The purpose of the present investigation is to ascertain the variation within the species, both recent and fossil, its distribution within the State both at present and during the Pleistocene period, and its range in geological time.

The material for the investigation consists of several hundreds of specimens from Illinois colletced by Daniels, Hinkley, Nason and by members of the State Natural History Survey, as well as of many lots from regions outside the State. The fossil material consists principally of collections made by field parties of the Illinois State Geological Survey.

The nature of the variation in size and other features was determined by the biometric method and the measurements are plotted on graphs (Figs. 2-16) to determine the mean of variation—the mode. In this, actual measurements have been used rather than averages. By this means the largest and smallest variations may be compared for each lot and subject. As measure-

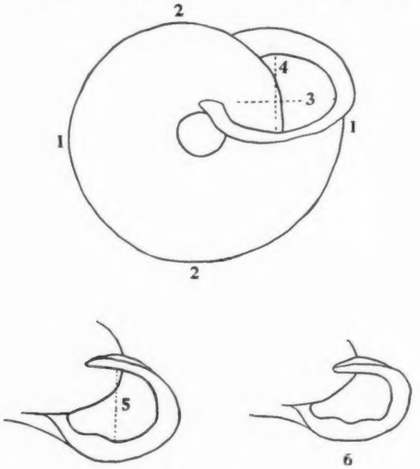
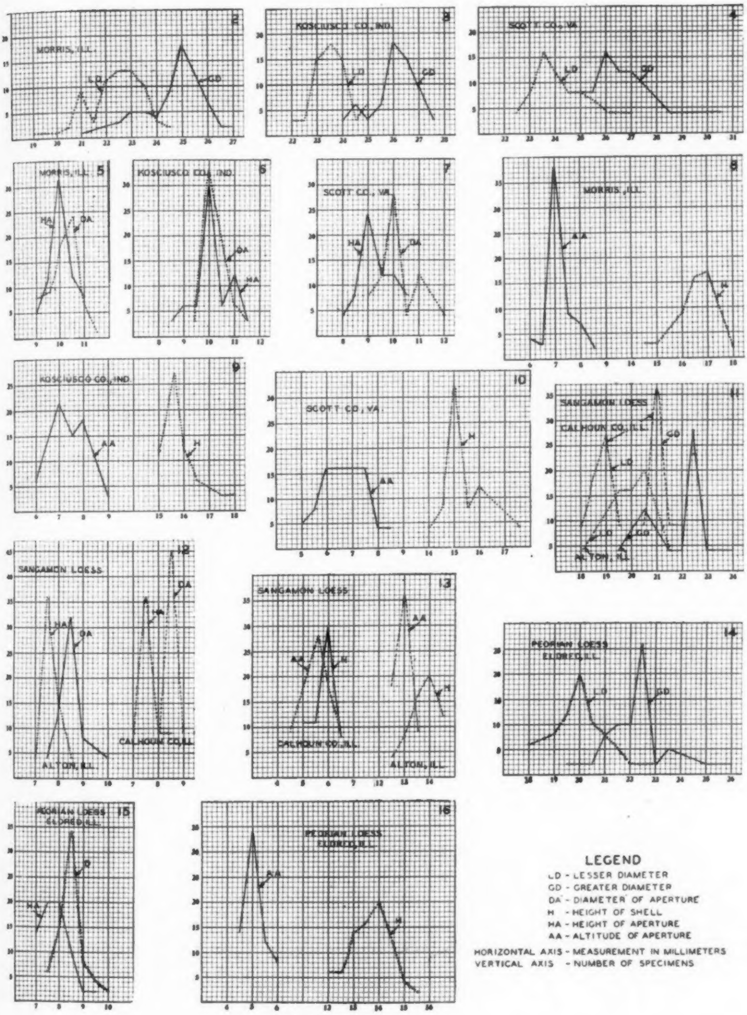


Fig. 1

* Contribution from the Museum of Natural History, University of Illinois, No. 73.


MORRIS, ILL.
KOSCIUSCO CO., IND.
SCOTT CO., VA.
SANGAMON LOESS
CALHOUN CO., ILL.
ALTON, ILL.
PEORIAN LOESS
ELDRED, ILL.
LEGEND
LD - LESSER DIAMETER
GD - GREATER DIAMETER
DA - DIAMETER OF APERTURE
H - HEIGHT OF SHELL
HA - HEIGHT OF APERTURE
AA - ALTITUDE OF APERTURE
HORIZONTAL AXIS - MEASUREMENT IN MILLIMETERS
VERTICAL AXIS - NUMBER OF SPECIMENS

FIGS. 2 - 16

ments are not always made from the same parts of the shell by all students it has been thought proper to indicate the method used in this investigation. In figure 1, 1-1 indicates greater diameter; 2-2, the lesser diameter; 3, the diameter of aperture; and 4, the height of aperture. Another measurement of great value which has been called the altitude of the aperture is indicated in 5 (Fig. 1). The value of this measurement may be noted by comparing the apertures of 5 and 6 (Fig. 1). This index is also different from the height shown in 4 (Fig. 1).

The graphs (Figs. 2-16) which have been made by plotting the measurements, show (1) the number of specimens of similar size in each group, (2) the mean of these measurements, that group having the greatest number of specimens, is shown as a norm or mode. In the graphs, the number of specimens examined is shown in the vertical column at the left, and the size in millimeters at the bottom.

Variation in the Recent Form of the Species

Specimens of the recent form have been plotted from the following localities: Morris, Illinois; Vauter Park, Kosciusko Co., Ind.; and Scott Co., Va.

Comparison of Diameters.—The shells from Morris, Illinois, have a greater diameter varying from 21 mm. to 27 mm., the norm (mode) being at 25 mm. The lesser diameter varies from 19 mm. to 24.5 mm. with two norms, one at 21 mm. and the other at 22.5 mm. (Fig. 2). In the Vauter Park lot, the greater diameter varies from 24 mm. to 27.5 mm., the norm being at 26 mm. The lesser diameter varies from 22 mm. to 25 mm. with the norm at 23.5. (Fig. 13). The greater diameter of the Scott Co. shells varies from 25 mm. to 30.5 mm. with the norm at 26 mm. and the lesser diameter varies from 22.5 mm. to 27 mm. with the norm at 23.5 mm. (Fig. 4).

Comparing the curves of diameter as shown in the table below we observe practical agreement in the norm (mode) among the representatives from the three localities.

	No. of specimens	Greater diameter	Lesser diameter
Morris, Illinois	68	25 mm.	22.5 mm.
Vauter Park, Indiana	63	26 mm.	23.5 mm.
Scott Co., Virginia	68	26 mm.	23.5 mm.

The Morris group indicates a positive tendency to form a bimodal graph and the other groups show a faint tendency in this direction.

Comparison of Apertures.—Height and diameter are considered in these measurements (Fig. 1). In the Morris lot the height varies from 9 mm. to 11 mm., the norm at 10 mm., and the diameter varies from 9 mm. to 11.5 mm. with the norm at 10.5 mm. (Fig. 5). In the Vauter Park lot the height varies from 8.5 mm. to 11.5 mm., the norm being at 10 mm., with a lesser mode at 11 mm. and the diameter ranges from 9.5 mm. to 11.5 mm. with the norm at 10 mm. (Fig. 6). In the lot from Scott Co. the height varies from 9 mm. to 12 mm. with the norm at 10 mm. and a lesser norm at 11 mm.,

and the diameter varies from 8 mm. to 10.5 mm. with the norm at 9 mm. and a lesser norm indicated at 10 mm. (Fig. 7). The graphs are compared in the table below. The frequencies are the same as for the diameter graphs.

	Height	Lesser mode	Diameter	Lesser mode
Morris, Illinois	10 mm.	none	10.5 mm.	none
Vauter Park, Indiana	10 mm.	11 mm.	10.0 mm.	none
Scott Co., Virginia	9 mm.	11 mm.	10.0 mm.	11 mm.

The graphs of aperture measurements show practical agreement, the Scott Co. specimens departing but slightly from the average. A bimodal tendency is to be noted in the Vauter Park and Scott Co., lots and its absence from the Morris lot.

Altitude of Aperture.—The altitude of the aperture (Fig. 1, No. 5), brings out certain features of value. In the lot from Morris the altitude ranges from 6 mm. to 8.5 mm. with the norm at 7 mm. (Fig. 8), in the Vauter Park lot from 6 mm. to 9 mm., with the norm at 7 mm. and a lesser norm at 8 mm. (Fig. 9), and in the Scott Co. lot from 5 mm. to 8.5 mm. with a wide norm at 6 to 7.5 mm. (Fig. 10). The norms of the height are also in practical agreement, being for Morris, 7 mm; Vauter Park, 7 mm.; and Scott Co. 6-7.5 mm. The Scott Co. graph is peculiar in having a wide norm or mode from 6 mm. to 7.5 mm. The average, however, is about that of the other lots.

A comparison of the major modes of the altitude and diameter of the aperture gives the following result.

	Altitude	Diameter	Pec cent.
Morriss, Illinois	7 mm.	10.5 mm.	67
Vauter Park, Indiana	7 mm.	10.5 mm.	70
Scott Co., Virginia	7 mm.	9 mm.	78

The comparison of the major modes of the height and the diameter of the aperture gives the result noted below.

	Height	Diameter	Per cent
Morris, Illinois	10 mm.	10.5 mm.	95
Vauter Park, Indiana	10 mm.	10.0 mm.	100
Scott Co., Virginia	9 mm.	10.0 mm.	90

From the above we see that when all lots are averaged together the height of the aperture is 92 per cent of the diameter and the altitude of the aperture is 74 per cent of the diameter. The importance of the two kinds of measurements, height and altitude, is obvious.

Comparison of Height of Shell.—In the Morris group the variation in height is from 14.5 mm. to 18 mm., with the norm at 17 mm. (Fig. 8), in the Vauter Park group the variation is from 15 mm. to 18 mm. with the norm at 16 mm. (Fig. 9), and in the Scott Co. group the variation is from 14 mm. to 17.5 mm. with the norm at 15 mm. (Fig. 10). The Morris lot averages highest, 17 mm., and the Scott Co. the lowest, 15 mm. The Scott Co. lot also exhibits departure from the other lots in measurements previously noted.

Variation in the Fossil Form of the Species

P. profunda found in fossil deposits divides into two groups, one from loess deposits which differs constantly from the recent form and has been separated as a race called *pleistocenica,* and another form from old forest and silt beds which more nearly resembles the recent form. These are known from beds of supposed Sangamon age in Indiana, and from Early Wisconsin deposits in both Illinois and Indiana. As the averages of two lots of this form do not vary essentially from those given under the discussion of the recent form, no graphss have been made for them.

Curves of the Race pleistocenica.—Material from three localities has been studied, two from the Sangamon loess and one from Peorian loess. The two lots from the Sangamon loess are first considered.

Sixty specimens from the type locality, Alton, Adams Co., Ill., are compared with 63 specimens from Calhoun County, Ill. The greater diameter of the Alton lot varies from 19.5 mm. to 24 mm., with a decided double mode, the lesser at 20.5 and the greater at 22.5 mm. The lesser diameter varies from 18 mm. to 21.5 mm. with the norm at 20.5 mm. In the Calhoun Co. material the greater diameter ranges from 20.5 mm. to 22 mm. with the norm at 21 mm. and the lesser diameter from 18 mm. to 19.5 mm. with the norm at 19 mm. (Fig. 11). Thus the Calhoun Co. shells average smaller than the Alton shells, as shown in the following table.

Alton, Illinois: greater diameter, 22.5 mm.; lesser diameter, 20.5 mm.
Calhoun Co.: greater diameter, 21.0 mm.; lesser diameter, 19.0 mm.

The height of the aperture of the Alton lot ranges from 7 mm. to 8.5 mm. with the norm at 7.5 mm. and the diameter from 7.5 mm. to 10 mm. with the norm at 8.5 mm. (Fig. 12). In the Calhoun County lot the height of the aperture ranges from 7 mm. to 8.5 mm. with the norm at 7.5 mm. and the diameter from 8 mm. to 9 mm. with the norm at 8.5 mm. (Fig. 12). Both the Alton and the Calhoun lots have the same mode or norm for both height and diameter of aperture.

The altitude of the aperture of the Alton lot ranges from 5 mm. to 6.5 mm. with the norm at 6 mm. and the Calhoun County lot ranges from 4.5 mm. to 6.5 mm. with the norm at 5.5 mm. (Fig. 13). The Alton lot thus has a slightly higher altitude of aperture than has the Calhoun County lot.

The height of the shell (Fig. 13) ranges in the Alton lot from 12.5 mm. to 14.5 mm. with the norm at 14 mm. and in the Calhoun County lot from 12.5 mm. to 13.5 mm. with the norm at 13 mm. The Calhoun County lot has a relatively lower spire than the Alton lot.

The Peorian group consists of 68 shells from Edred, Green Co., Ill. from Peorian loess. The greater diameter ranges from 19.5 mm. to 26 mm. with a major norm at 22.5 mm. and a small minor norm at 23.5 mm. and the lesser diameter from 18 mm. to 23 mm. with the norm at 20 mm. (Fig. 14). The height of the aperture ranges from 7 mm. to 9.5 mm. with the norm at 8 mm.

and the diameter from 7.5 mm. to 10 mm. with the norm at 8.5 mm. (Fig. 15). The altitude of the aperture ranges from 4.5 mm. to 6 mm. with the norm at 5 mm. and the altitude of the shell ranges from 12 mm. to 15.5 mm. with the norm at 14 mm. (Fig. 16).

The following table permits a comparison of the two groups from the Sangamon loess with the group from the Peorian loess. The diameter of the shell of the Alton and the Eldred lots is smaller than that of the Calhoun lot, and the altitude of the aperture of the Calhoun County and the Eldred lots is smaller than that of the Alton lot. On the whole, however, there is substantial agreement between the modes of the three lots.

Comparative data on shells from Sangamon and Peorian Loess in Illinois:

	Alton	Calhoun Co.	Eldred
Greater Diameter	23.0 mm.	21.0 mm.	22.5 mm.
Lesser Diameter	20.5 mm.	19.0 mm.	20.0 mm.
Height of Aperture	7.5 mm.	7.5 mm.	8.0 mm.
Diameter of Aperture	8.5 mm.	8.5 mm.	8.5 mm.
Altitude of Aperture	6.0 mm.	5.5 mm.	5.0 mm.
Height of Shell	14.0 mm.	13.0 mm.	14.0 mm.

The following two tables show the normal modes of the altitude and height of the aperture as compared with the diameter:

	Altitude	Diam.	Pct.	Height	Diam.	Pct.
Alton	6	8.5	70.6	7.5	8.5	88.2
Calhoun Co.	5.5	8.5	64.7	7.5	8.5	88.2
Eldred	5	8.5	58.8	8	8.5	94.1

Comparison between the apertures of the Pleistocene loess shells *(pleistocenica)* and the recent shells is given in the table below. It will be observed that in all cases the loess shells have a smaller altitude mode or norm than the shells of the recent fauna and the shape of the aperture is constantly different. In size, the average percentage for the fossil shells is 64.7 and for the recent shells 68.7. The height-diameter of the aperture for the fossil shells averages 90.2 per cent and of the recent spcies 95 per cent.

Comparison of Apertures

	Alton	Cal. Co.	Eldred	Morris	Indiana	Virginia
Altitude	6.0	5.5	5.0	7.0	7.0	7
Diameter	8.5	8.5	8.5	10.5	10.0	10
Per cent	70.6	64.7	58.8	66	70	77
Height	7.5	7.5	8.0	10	10	9
Diameter	8.5	8.5	8.5	10.5	10	10

Comparison of Diameter and Height of Shell

	Alton	Cal. Co.	Eldred	Morris	Indiana	Virginia
Greater diameter	23.0	21.0	22.5	25	26.0	26.0
Lesser diameter	20.5	19.0	20.0	23	23.5	23.0
Height	14.0	13.0	14.0	17	15.5	15.0

Geographical Distribution of Recent and Pleistocene Profunda

The geographical distribution of *Polygyra profunda* in the recent fauna extends from Eastern Nebraska eastward to New York, Pennsylvania, and Maryland, and from Minnesota and Michigan southward to Missouri, Tennessee, Alabama, and North Carolina. It is apparently limited to the northern part of Illinois as far south as Fulton County (Fig. 17) but is abundant in Indiana as far south as Lawrenceburg and occurs also in Kentucky. The southern limit of its distribution apparently crosses north-central Illinois and

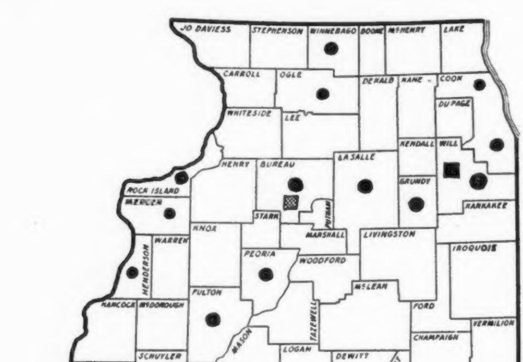


Fig. 17

then turns abruptly to the southeast across Indiana. The southern distribution in Virginia, Alabama, etc., is in mountain regions.

Pleistocene distribution.—*P. profunda* of the Pleistocene period includes both the typical form and the variety *pleistocenica*. The fossil race in its typical form has been found thus far only in western and southwestern Illinois in regions bordering Mississippi River (Fig. 17). A somewhat intermediate form has been collected in Monroe County. No typical *pleistocenica* has been seen outside of Illinois, but the form so abundant in the Peorian loess of Iowa is believed to belong to this race.

True *P. profunda* has a wide distribution as a Pleistocene fossil, its range extending from Iowa southward to Missouri and southern Mississippi and eastward to Ohio. In Illinois its distribution is from Will County to Union and Gallatin counties (Fig. 17). It will be observed that the Pleistocene distribution is far to the south of the recent distribution, indicating that during the Pleistocene or Glacial period the geographic distribution extended much farther southward in the Mississippi Valley than at the present time. What factors were involved in this southward extension are not definitely known, although it might have been from climatic causes.

Range in Geological Time

P. profunda is recorded from one doubtful Aftonian deposit in Harrison County, Iowa (Geol. Iowa, vol. 20, pp. 365-366) and from one Yarmouth deposit at Council Bluffs, Iowa, (Op. Cit., vol. 11, pp. 258-267), by Shimek. Gregor (Nautilus, vol. 30, pp. 64-66) also records *P. profunda* from a Callaway County deposit in Missouri. In Illinois Aftonian deposits are very rare and thus far no *P. profunda* has been observed from this interval. Yarmouth deposist are widely distributed over southern and central Illinois and a large fauna is represented, but no specimen of *P. profunda* has been seen in more than a hundred different deposits examined. This absence of so large and conspicuous a species from a geological horizon well developed and carefully studied in Illinois is noteworthy, and if sustained by additional investigation shows a very peculiar geological distribution of this species.

Beginning with the Sangamon interglacial interval, *P. profunda* becomes a more or less abundant species in Illinois and Indiana. The horizon of the deposits in Mississippi, Misouri, and Arkansas have not been definitely correlated with those farther north. In the Wisconsin series, *P. profunda* is abundantly represented from Peorian, Shelbyville, and later deposits. The race *pleistocenica* is known in Illinois from Sangamon to Peorian time.

Summary

Polygyra profunda in the recent fauna has a large shell with an almost round aperture. In Pleistocene time a race lived which averaged smaller than the recent form with a more elongated aperture, espcially when viewed from the front of the shell. The average index (mode or norm) of each is show below.

	Greater Diam.	Height of Aperture	Altitude of Aperture
Recent	25.7 mm.	9.6 mm.	7 mm.
Fossil	22.2 mm.	7.6 mm.	5.5 mm.

The Pleistocene race has been differentiated as variety *pleistocenica* F. C. Baker and occurs in deposits of Sangamon, Peorian, and Shelbyville age in Illinois, the localities being near or bordering Mississippi River. The race also lived in Iowa and has been found in Peorian loess. Typical *P. profunda* is distributed geographically throughout northern Illinois only but its distribution in the United States ranges from eastern Nebraska eastward to New York and Maryland and southward across central and southern Indiana and Kentucky, to North Carolina and northern Alabama. During Pleistocene time, however, *P. profunda* is known to have been distributed as far south as Missouri and southern Mississippi and from Iowa eastward to Ohio. Some of these fossil records may be referable to the race *pleistocenica*. In Illinois, *P. profunda* was abundant as far south as Union County. This difference in the geographical distribution in recent and Pleistocene time indicates an extension of the species in the Mississippi Valley of about 600 miles of the present Illinois range and about 300 miles south of the Kentucky localities.

The geological range in Illinois is from the Sangamon interglacial interval, but in Iowa and Missouri it has been recorded from deposits believed to be of Aftonian and Yarmouth age. It has not been found in Illinois in deposits earlier than the Sangamon.

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DIGESTIVE RATES OF MARINE INVERTEBRATES

ELTON R. EDGE

The object of this work was to determine the time required for food to pass through the digestive tract of various marine invertebrates. Riddle (1909) by a more exact method has made a study of the rate in lower vertebrate forms, but there appeared to be little or no data on invertebrates although Moore (1912) has considered their food requirements.

Two methods of approach were employed. One was to keep the animal in filtered sea water until the faeces were no longer passed, then give it normal or acceptable food and time the appearance of the faeces. A second method, the one normally used, was to introduce powdered carmine along with the food and check the time of its appearance in the faeces. The latter method worked well with voracious and generally rapid moving aggressive animals such as crabs, certain annelids, octopi and the like whose appetite seemed little effected by new and possibly uncongenial surroundings. But with the passive, non-aggressive forms whose chief response to adverse conditions was withdrawal into a shell, burrow or contracted condition, the first method or a combination of the two was resorted to.

The chief objection to the first method was the ultra normal rate at which food sometimes passed through the empty digestive tract. When no food was passing through the alimentary canal at the time carmine food was given, the first trace of carmine in the faeces although timed was disregarded, while the time of normal appearing faeces containing a large amount of carmine was regarded as indicative of the normal rate. In some animals traces of carmine would continue in the faeces for a considerable period after its first appearance. This was particularly noticeable in the keyhole limpet, *Megathurea,* in which carmine first appeared in the faeces seven hours after feeding, but bits of carmine and bryozoan plates upon which the animal had been feeding continued to be passed for more than seventy-two hours after isolation of the animal from any food supply. Results of a similar nature were obtained with the sea urchin *Lytechinus*. The size of the animal in some cases made a difference in the digestive rate. In the tunicate *Ciona,* the large individuals required a longer time to show carmine than the smaller ones. The difference was not regular but was in the neighborhood of one hour. As various authors have pointed out temperature exerts a decided influence on the digestive rate. The passage of carmine through the tunicate *Ciona* was almost doubled by increasing the temperature from 21°C. to 28°. The rates given in the table are for the normal average temperature of the aquarium water 20° C. It was also noted that some variability in rates occurred with the same species of animal under what appeared to be uniform conditions as regard its temperature and physical surroundings. Activity on the part of the animal

seemed in some cases to influence the rate at which food passed. The annelid *Nereis* passed carmine at a somewhat shorter interval, if it was made to move about freqeuntly, than if it remained inactive after feeding. It has not been definitely established in all cases that carmine does not change the rate at which food passes through an animal, but where checks were made the rate was not altered.

TABLE I

	Time interval in hours	Remarks
Annulata		
Nereis vexillosa	33	Inactive after feeding.
Terebellid, *Amphitrite* sp.?	8	
Echinodermata		
Asterina miniata	8	Bits carmine mucus occasionally 3 hrs.
Lytechinus animesis	11	Trace cormine may continue more 48 hrs.
Stichopus californicus	11	
Molpadia arenicola	5	Not very satisfactory.
Ophioderma panamensis	10	
Arthropoda		
Balanus tintinabulum	6	
Ligyda occidentalis	6	
Ligyda occidentalis	7	
Orchestoidae californiana	5	
Spirontocaris palpator	3.5	
Panulirus interruptus	5	Trace carmine 2 hrs.
Callianassa californiensis	6	Considerable variability
Pagurus samuelis	6	
Lepidopa myops	6.5	
Pachygrapsus carripes	5	
Cancer anthonyi	11	Irregular
Mollusca		
Ostrea lurida	3	Trace 2 hrs.
Mytilus californianus	3	
Cardium quadragenarium	11	
Schizothaerus nuttalli	3	
Paphia staminea	5	Trace earlier, shell closed 10 or more.
Zirfaea gabbi	3	
Macoma yoldiformis	6	
Alectrion fossata	5	
Megathura crenata	6.5	May continue more 72 hrs.
Tethys californica	11	
Protobranchus californicus	12.5	
Hermissenda crassicornis	2	Not very satisfactory
Polypus bimaculatus	4	Trace earlier
Tunicata		
Ciona intestinalis	7	

A study of the table indicates that animals whose food is made up in a large part of plants, in general retain food in the alimentary canal for longer periods than purely carniverous forms. In the former group are such echinoderms as *Lytechinus* and *Stichopus* and molluscs like the sea hare *Tethys.* The active predaceous forms such as the octopus, and crustaceans such as certain of the crabs and shrimps using animal matter as food, retain it for a much shorter period than the vegetarians. The current feeders like most of the pelecypoda, however, even though algae and diatoms constitute a large part of their food, have even a shorter period than the carnivora which is probably due to the minute size of this food. One or two irregularities occur *Nereis xevillosa,* a carnivorous form, retained clam gills or bits of worms for thirty hours or more but during that time was inactive. The pelecypoda, *Cardium quadragenarium,* retained food material for a considerably longer period than any of the other bivalves observed.

Grateful acknowledgment is made for research facilities provided by the William G. Kerckhoff Marine Laboratory, and for assistance and advice received from its director, Prof. G. E. MacGinitie.

Summary

1. The digestive rates of a number of marine invertebrates were investigated by timing the passage of food through the animal.

2. In general, animals which utilized plant food of macroscopic size had a time interval of about eleven hours.

3. Active carnivorous forms averaged about six hours.

4. Current feeders averaged three or four hours.

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DISTRIBUTIONAL RECORDS OF REPTILES AND AMPHIBIANS IN OKLAHOMA

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The following records are based largely upon specimens, designated by KU, in the Dyche Museum of Natural History, of Kansas University. Dr. E. H. Taylor of the same university, Mildred Parker of Drumright, Oklahoma, and J. A. Wilson of Alva, Oklahoma, have collected many of these. Others were collected by the junior author during September, 1933, and by the senior author during July of 1931 (some of the specimens in this collection designated by HMS, retained by the collector) and during July and September of 1933 (some of these also retained). Further data have been obtained from specimens, designated by EHT & HMS, collected by Dr. E. H. Taylor and the senior author during the early part of June, 1932. Forty-seven species are represented in these collections.

Sixty-five new county records are incorporated in the following notes. Among these are records of four species new to the state: *Sceloporus spinosus floridanus, Tantilla nigriceps, Scaphiopus couchii* and *Gastrophryne olivacea, Liopeltis vernalis* is also reported as new. The locality data for the latter, however, is merely "Southern Oklahoma." The most surprising of these records is that of the *Scaphiopus,* which has apparently been reported from no nearer Oklahoma than 50 miles south of Fort Worth. (Kellogg, 1932). The *Sceloporus* has previously been reported from no farther north than Tarrant county, Texas (Strecker, 1929), although Dr. Taylor has collected specimens of it just across the border near Gainesville, Cooke county, Texas (KU 12641). *Gastrophryne olivacea* is likely new only in name.

The list of species follows. New records are starred.

1. *Scaphiopus bombifrons* Cope. *Cleveland county, 2 mi. N. of Lexington (EHT & HMS). *Pawnee county, Cleveland (KU).

This species, characterized by the presence of an interorbital boss, together with a more or less rounded, not elongated, metatarsal tubercle, is here considered specifically distinct from *hammondii hammondii,* the ranges of which presumably overlap at least in western Oklahoma, and probably through eastern New Mexico and western Texas. A complete explanation of the consideration of this form as specifically distinct will be forthcoming in the future in a report on the amphibians of Kansas.

2. **Scaphiopus couchii* Baird. Tillman county (KU).

A single specimen of this species has been obtained from Dr. A. I. Ortenburger. In New Mexico the species has been reported from only the extreme southwestern corner (Van Denburgh, 1924) and in Texas from no farther north than 50 miles south of Fort Worth (Kellogg, 1932).

3. *Scaphiopus hammondii hammondii* Baird. *Woods county, Alva (KU).

A single, immature specimen 26 mm. in length of head and body is in the Dyche Museum. An examination of a large series of *bombifrons* has definitely shown that the interorbital boss, which is absent in this specimen, is a character of variation neither with age nor with sex. Young *bombifrons* possess as distinct bosses as adults, and there is no variation between males and females in this respect. For these reasons, and numerous others to be considered elsewhere, this specimen is considered as *hammondii*. It is the only one examined (by the senior author) upon which at present the overlapping so far east of the two species can be based. Overlapping in western New Mexico is shown by a number of specimens of both species, breeding together in the same pools, collected by Dr. Taylor in Valencia and Grant counties.

The only other record of this or the preceding species are from Cimarron county (Ortenburger, 1927; Ortenburger and Freeman, 1930) and Payne county (Ortenburger, 1926).

4. *Scaphiopus holbrookii holbrookii* (Harlan). *Cleveland county, 2 mi. N of Lexington (EHT & HMS).

A series of this species was collected at night in temporary pools in pastures on June 3, 1932, a day or two after a period of rains which flooded the surrounding country. They were in full chorus, and associated with *Bufo woodhousii woodhousii, Bufo cognatus, Scaphiopus bombifrons* and *Pseudacris clarkii.*

The two species of *Scaphiopus* collected here differ markedly in several respects, in spite of some convergent characters. An interorbital boss is present in each, but in *h. holbrookii* the crest of the boss is far back of the eyes, while in *bombifrons* it is between them. The metatarsal tubercles are much elongated in the former, while in *bombifrons* it is more or less rounded as in *hammondii* or *couchii.* Males of *holbrookii* possess two mammae-like projections from the ventral surfaces in the pectoral region. Its call is higher pitched, less guttural, shorter and not so loud as that of *bombifrons*, and the vocal pouches, when inflated, are smaller and slightly constricted longitudinally in the middle. When singing they do not float with legs outstretched in the water, as *bombifrons* habitually does, but select stations near little projections of land, where they are seated while calling.

5. *Bufo cognatus* Say. Cleveland county, Norman (KU), 2 mi. N. of Lexington (EHT & HMS), *Grant county, 2 mi. N. of Pond Creek (HMS).

The specimens from near Lexington were collected with the *Scaphiopus holbrookii.* Males were singing. The Pond Creek specimens were all small, and were found hopping about during the afternoon in sandy, grassy ravines.

Previous records for this species are Cleveland county (Ortenburger, 1926), Caddo county *(op. cit.)* and Noble county (Burt, 1931).

6. *Bufo woodhousii woodhousii* Girard. Cleveland county, 2 mi. N. of Lexington (EHT & HMS), Comanche county, Lawton (HMS). *Grant county, 2 mi. N of Pond Creek (HMS). Pawnee county, Cleveland (KU). Woods county, 3 mi. N of Faulkner (KU).

The single male specimen from Cleveland county was collected with numerous other anurans in temporary pools in pastures. It was not singing.

Woodhousii is here considered to be related sub-specifically to *fowleri*. Full details are to be presented in the future.

7. *Acris gryllus* (Le Conte). Blaine county, 1 mi. SW of Canton (KU). *Creek county (KU). *Major county, Corbin Ranch, 28 mi. NW of Fairview. *Ottawa county, Pitcher (KU).

8. *Pseudacris clarkii* (Baird). Creek county, Sapulpa (KU). *Cleveland county, 2 mi. N of Lexington (EHT & HMS).

The numerous dorsal spots and the grayish ground color distinguish this species from other forms reported from Oklahoma and adjacent states. It has been definitely reported previously by Cope (1893) from Le Flore county, and by Burt (1932) from Kay county. Ortenburger's (1926) *nigrita* from Creek county is no doubt the same.

9. *Rana catesbeiana* Shaw. Cleveland county, Norman (KU). *Dewey county, 10 mi. NW of Canton.

10. *Rana sphenocephala* (Cope). Cleveland county, Near Norman (KU).

11. **Gastrophryne olivacea* (Girard). *Washington county, Bartlesville (KU).

This is apparently the first record of *olivacea* for Oklahoma. The specimen is certainly not *carolinensis,* the species previously reported from Oklahoma. It is possible that some of the central Oklahoma records of the latter species should in reality be of the former.

12. *Crotaphytus collaris* (Say). Creek county, Drumright (KU). Murray county, Near Sulphur (KU). Okmulgee county (KU). *Osage county (KU).

This species has been reported from all parts of the state.

13. *Holbrookia maculata maculata* (Girard). *Comanche county, Near Lawton (HMS). *Harper county, Cimarron River, S of Englewood, Kansas (HMS). *Woods county, 12 mi. W of Alva (KU).

This species was first reported within the state by Cope (1893) from Fort Supply. All recent records are from western and northwestern Oklahoma.

14. **Sceloporus spinosus floridanus* (Baird). *Love county, Near Marietta (KU).

This species has apparently not been reported before from Oklahoma. Three specimens were collected by Dr. E. H. Taylor in the summer of 1930.

15. *Sceloporus consobrinus consobrinus* (Baird and Girard). *Cotton county, 1 mi. N of Red River (HMS). Comanche county, Near Lost Lake, Wichita Mts. (HMS). Creek county, Drumright (KU), Near Sapulpa (KU). *Dewey county, 5 mi. SW of Canton (KU). *Love county, Near Red River (KU). Okmulgee county (KU).

Reported from only a few widely separated localities in the state.

16. *Phrynosoma cornutum* (Harlan). *Choctaw county (KU). Creek county, Drumright (KU). Comanche county, Near Lawton (HMS). Dewey county, 5 mi. SW of Canton (KU). *Woods county, Alva (KU).

Cope (1893) first reported this species for the state, from specimens taken near Fort Supply and Kingfisher, I. T.

17. *Ophisaurus ventralis* (Linné). *Woods county, 12 mi. W of Alva (KU).

Recent reports of this species are meager and from widely separated localities in the state. First reported by Cope in 1893.

18. *Cnemidophorus sexlineatus sexlineatus* (Linné). Comanche county, Near Lawton (HMS). *Cotton county, 1 mi. N of Red River (HMS). Creek county, Drumright (KU). Dewey county, 5 mi. SW of Canton (KU). *Grant county, 2 mi. N of Pond Creek (HMS). *Harper county, Cimarron River, S of Englewood, Kansas (HMS). *Love county, Red River Bridge near Marietta (KU). Woods county, 12 mi. W of Alva (KU).

19. *Leiolopisma laterale* (Say). *Dewey county, 5 mi. SW of Canton (KU). Okmulgee county (KU).

The specimen from Dewey county represents the northwestern limit of its known range in Oklahoma.

20. *Eumeces fasciatus* (Linné). Okmulgee county, Okmulgee (KU). *Washington county, near Bartlesville (KU).

21. *Eumeces obsoletus* (Baird and Girard). *Murray county, Sulphur (KU). Woods county, Alva (KU).

22. *Eumeces septentrionalis* (Baird). *Woods county, 12 mi. W of Alva (KU).

A record from Tulsa county (Force, 1928, 1930) is the only other from the state.

23. *Diadophis punctatus arnyi* (Kennicott). Murray county, Sulphur (KU).

Most common in eastern and southern Oklahoma. First reported from the state by Cope in 1893.

24. *Heterodon contortrix* (Linné). *Harper county, Cimarron River, S of Englewood, Kansas (HMS). *Woods county, 12 mi. W. of Alva (KU).

The single specimen from Harper county was found shortly before dusk crossing the dunes just north of the Cimarron River. The track was trailed

about 300 feet before the snake was found. The trail of this species is broad and the undulations are closely approximated, in sharp contrast to the trail of *Arizona*, also found there, which is quite narrow, the undulations spaced far apart and the sand but slightly displaced in the forward movement.

This is apparently the farthest west the species has been recorded.

25. *Heterodon nasicus* Baird and Girard. *Woods county, 12 mi. W of Alva (KU).

26. **Liopeltis vernalis* (Harlan). Southern Oklahoma (KU).

This is apparently the first record of the species from Oklahoma.

27. *Coluber constrictor flaviventris* (Say). Creek county, Drumright (KU). Washington county, Bartlesville (KU). Woods county, 12 mi. W of Alva (KU).

28. *Masticophis flagellum flagellum* (Shaw). Love county, near Gainesville, Texas (KU).

Collected by Dr. Taylor in the lowlands on the north side of the river.

29. *Masticophis flagellum flavigularis* (Hallowell). *Beaver county, 8 mi. E and 4 mi. S of Beaver (KU). *Dewey county, 5 mi. SW of Canton (KU). Woods county, 12 mi. W of Alva (KU).

30. *Elaphe obsoleta confinis* (Baird and Girard). Creek county, Drumright (KU).

31. *Arizona elegans elegans* (Kennicott). *Harper county, Cimarron River, S of Englewood, Kansas (HMS).

The two specimens were found in the sand dunes just north of the river at about 10 o'clock in the evening. The species has previously been reported in the state from Woods county (Ortenburger, 1925).

32. *Pituophis sayi sayi* (Schlegel). *Dewey county, 5 mi. SW of Canton (KU). Woods county, 12 mi. W of Alva (KU).

33. *Lampropeltis calligaster* (Harlan). Creek county, Drumright (KU). *Washington county, near Bartlesville (KU). Woods county, 12 mi. W of Alva (KU).

34. *Rhinocheilus lecontei* Baird and Girard. *Woods county, 12 mi. W of Alva (KU).

A record from Harman county (Ortenburger and Freeman, 1930) is the only other report of this species from the state.

35. *Sonora semiannulata* Baird and Girard. Creek county, Drumright (KU). *Payne county, Stillwater (KU). *Woods county, 12 mi. W of Alva (KU).

36. *Natrix grahamii* (Baird and Girard). *Comanche county, Wichita Mountains (HMS).

Mr. Jim Slack of Tulsa and the senior author collected a single specimen at night along a mountain stream.

37. *Natrix rhombifera* (Hallowell). Comanche county, Wichita Mountains (HMS).

Large numbers were collected at night along mountain streams by Mr. Jim Slack and the senior author.

38. *Natrix transversa* (Hallowell). Comanche county, Wichita Mountains (HMS). Creek county, (Drumright (KU). *Payne county (KU).

Several specimens were collected in the Wichita Mountains with *Natrix rhombifera* and *grahamii.*

39. *Potamophis striatulus* (Linné). *Love county, near Gainesville, Texas (KU).

40. *Tropidoclonion lineatum* (Hallowell). *Muskogee county, near Muskogee (KU).

41. *Thamnophis sauritus proximus* (Say). *Creek county, Drumright (KU).

42. *Tantilla gracilis* Baird and Girard. *Payne county, near Drumright (KU), Stillwater (KU).

Details of scalation follow:

Upper labials	6-6	6-6	6-6
Postoculars	1-1	1-1	1-1
Ventrals	122	137	127

In all three specimens the head is but slightly darker than the dorsal surface of the body.

43. **Tantilla nigriceps* Kennicott. *Payne county, Drumright (KU). *Woods county, Alva (KU).

Details of scalation follow:

Upper labials	7-7	7-7	7-7
Postoculars	2-2	2-2	2-2
Ventrals	144	150	156

The color of the dorsal surface of the head in each of the three specimens is black, and is sharply demarcated from the lighter color of the body. In one specimen (Woods county) the black extends posteriorly from the head over four scale rows; in the other two it extends over but one to two.

44. *Chelydra serpentina* (Linné). *Le Flore county (KU).

45. *Kinosternon flavescens* (Agassiz). Alfalfa county, 3 mi. NW of Augusta. *Comanche county, Lawton (HMS). *Dewey county, 5 mi. SW of Canton.

Specimens were found in the sewer drain at the Agricultural Experiment Station in Lawton.

46. *Terrapene carolina triunguis* (Agassiz). *Creek county, 16 mi. N of Bristow (EHT & HMS). *Payne county, Stillwater (KU).

47. *Terrapene ornata* (Agassiz). Alfalfa county, 2 mi. S of Aline. *Blaine county, 3 mi. E of Canton (KU). *Dewey county, 5 mi. SW of Canton (KU). *Harper county, Cimarron River, S of Englewood, Kansas (HMS). *Murray county (KU). *Payne county, Stillwater (KU). *Woods county, 12 mi. W of Alva (KU).

This report has been made possible through the courtesy of Mr. C. D. Bunker, curator of Dyche Museum of Natural History, of the University of Kansas. Our appreciation for this is expressed here. We are further indebted to Dr. E. H. Taylor for various valuable suggestions and criticisms.

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TWO UNUSUAL WOODCHUCK SKULLS

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During the last year two skulls of the woodchuck *Marmota monax monax* (Linnaeus), both from Illinois, have come into my possession, each showing unusual dental conditions which are interesting and worthy of brief note. Both skulls are reminiscent of those described by Wagner (1923) and Thorpe (1930).

Skull No. 1 (Figs. 1-3) was sent to the zoology department from Georgetown. The skull is practically entire and all four incisors are present. The upper right incsoir is the offender in this case. It emerges from the alveolus in the premaxilla with an extreme leftward trend. In consequence of this growth in a wide-spread instead of a tight spiral form, it has missed piercing the skull, and has grown off to the left side of it. In passing the left maxilla, however, it just touched the anterior lateral region of this bone and here caused an irritation anterior and mesial to the interorbital foramen. The irritation has produced an excessive growth of the bone at this point, pushing the left infraorbital foramen upward and outward, so that the incisor passes through a groove of bone as it curves upward. At the point where contact between the upper and lower incisors would normally occur, this upper right incisor shows a worn outer enamel surface where it comes in contact wtih the inner surface of the lower *left* incisor. The upper left incisor shows the same left shift exhibited by the upper right incisor, starting its curve to the same degree, but unfortunately it is broken off at a point 23 mm. beyond the emergance from the alveolus, the break being old. Every indication is that it swung to the left, duplicating the curvature of the right incisor and matching it in all respects. The lower incisors (Fig. 2) have grown to a length of 55 mm., but their alignment is correct and normal, though the space between them is a trifle wide; they are deflected neither to the right nor to the left. When the jaws are assembled in their normal position, the distal tips of these teeth reach just above the tip of the nasal bones, the lower right incisor just nicking the anterior tip of the right nasal. The left tooth extends 2 mm. beyond the tip of the left nasal due to the contact with the right upper incisor which has pushed it forward. The molars make normal contact and show normal wear. There is no evidence of disease or accident and the condition is undoubtedly congenital. The skeleton of the animal was found in a hollow log, and the cause of death is problematical.

Skull No. 2 (Figs. 4-5) was found by the writer near Urbana. Only the skull was found and the lower jaw and right upper incisor are missing. The left incisor is seen to pierce the roof of the mouth, forming a large foramen on the intermaxillary suture in the anterior half of the maxillary bones. Coming out into the nasal cavity exactly on the mid line, the tooth has shattered the anteriod third of the mesethmoid and the anterior quarter of the

ethmo-turbinals, the latter particularly on the right side because of the curvature of its growth. The tooth then emerges from the right external naris to start its second loop, the curvature of which exactly corresponds to that of the first loop which in turn is more acute than the curve of the normal tooth. The outside diameter of this loop is 24 mm. That the animal had little difficulty in closing its mouth is indicated by the uniform wear of the crowns of the molars. What the condition in regard to the right incisor must have been can be surmised by evidence of the skull itself. It, too, had a right shift, for there is a deep furrow through the ventral half of the premaxillary, extending obliquely downward and backward across the anterior ventral third of the right maxilla, exposing the alveolus of the second molar on that side. The direction of this furrow corresponds to the angle of shift of the left incisor. So deep is this groove that the maxilla at one point has begun to roof it over. The mesial wall of the right premaxilla has been shattered. There is no indication of disease or accident evident and no indication of the growth form of the lower incisors: they at least made no contact with the skull. The condition was probably congenital.

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Figs. 1-3. Skull Number 1. Fig. 1. Ventral view of skull. Fig. 2. Mandibles. Fig. 3. Lateral view of skull from the left side.
Figs. 4-5. Skull Number 2. Fig. 4. Ventral view of skull. Fig. 5. Lateral view of skull from the right side.

BOOK REVIEWS

RASSENKUNDE UND RASSENGESCHICHTE DER MENSCHHEIT, by Egon Freiherr von Eickstedt. Ferdinand Enke Verlag, Stuttgart. VIII + 936 pp., 613 illustrations, 3 tables and 8 colored plates. 1934. RM: 76,50.

This is a work that no student of anthropology can afford to disregard, for while not all the conclusions offered seem to this reviewer to be equally sound, yet even when full consent does not appear to be warranted, the views of the author invite serious consideration and his manifest scholarship compels respectful suspension of judgment. Anyone who in the future attempts serious research in anthropology will be obliged to consult this volume to acquaint himself with the author's theoretical speculations as well as to give due attention to his practical interpretations.

The treatment followed in the volume represents a radical departure from that which has come to be regarded as traditional. This is so because the author believes that the conventional methods of the discipline are inadequate because they are too provincial to meet the requirements of present-day anthropology. He insists that the problems that concern this science are primarily biological and not historical. To be sure, history must still furnish the background for investigation, but research must take into account man's ancestry, his environment and his future destiny if the resulting story is to make even a pretense at completeness. It will, therefore, be necessary not merely to present the facts of man's history but also to interpret these facts in relation to one another as well as in relation to the suppositions upon which theoretical conclusions from them rest. Anthropology must no longer be thought of as the science of man considered as an individual, but that science must study man as a racial entity. This discipline is, therefore, a kind of morphology of the Hominiidae, and the races of man must be considered as morphological units of mankind. Accordingly, the notion of species must be broadened so as to take into account physiological criteria which can be experimentally established.

The chapter on the origin and development of man warrants careful study. The author states, too daringly perhaps, that man's origin and development are riddles no longer. He admits, however, that many questions still remain unanswered concerning the details of this origin and development. Nor does he hesitate to use the word *miracle* in speaking of the force which underlies and directs all this activity.

The arguments from comparative anatomy and palaeontology for the evolution of the human body are presented very briefly. This is a significant departure from the usual prolix presentation.

As causes of variation, the author recognizes two factors: an internal capacity for variation, and an external causative environmental factor. In the development of his ideas concerning these factors, the author follows Lamarck, who, he insists, is really a Darwinian. Natural selection, in the Darwinian sense, is dismissed as a short-lived and superficial factor, while sexual selection is almost totally discredited.

As a dominant causative factor in the production of mutations, the author presents a "capacity for development" (Entwicklungskapazität). He assumes that mutations that arise independently of each other and according to no plan whatever may so combine as to form systems of organs or even modify existing organs. This is a gratuitous assumption.

The problems connected with the original geographical habitat of man receive full and careful treatment. There is a list of the various localities that have been suggested as possible places of origin, and the claims of each are critically examined. The author's conclusion is that man may claim central Asia as his original home, and the middle or late Tertiary period as the time of his arrival at man's estate.

The volume may easily and naturally be divided into two parts. The portion thus far reviewed is the first part, and the rest of the book, which is the text proper, is the second part. It is hard to speak of the merits of this second part without using superlatives. The illustrations—and there are many—really illustrate the text. The subject matter is presented clearly and completely. If there is a better treatment extant this reviewer has never seen it. This book is a monument in its generation. —F. J. Wenninger.

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